United States Department of State

S1.2:EC 7/4

Coupling of Ecological Studies with Remote Sensing

IGIN

COMPLETED

U.S. MAN AND THE BIOSPHERE PROGRAM

BEST COPY AVAILABLE

Cover photograph assembled from AVHRR imagery courtesy C. J. Tucker, GIMMS/GSFC, Goddard Space Flight Center, Greenbelt, Maryland 20771.

The U.S. Man and the Biosphere Program (U.S. MAB) is an interdisciplinary research, education and training program on the relationship of people to their environment. U.S. MAB is supported by the United States Department of State, United States Department of Interior-National Park Service, United States Department of Agriculture-Forest Service, National Aeronautics and Space Administration, National Oceanic and Atmospheric Administration, the Peace Corps and the Smithsonian Institution. The opinions, conclusions and recommendations expressed in this publication are those of the authors and do not necessarily reflect the views of the participating agencies and institutions. Inquiries concerning the U.S. MAB Program should be addressed to the Executive Director, U.S. MAB Secretariat, OES/ENR/MAB, United States Department of State, Washington, D.C. 20520.

DEPARTMENT OF STATE PUBLICATION 9504
Bureau of Oceans and International Environmental
and Scientific Affairs

Released September 1986

NOV 28 [illegible]

S1.2:Ec7/4

COUPLING OF ECOLOGICAL STUDIES WITH REMOTE SENSING: POTENTIALS AT FOUR BIOSPHERE RESERVES IN THE UNITED STATES

U.S. MAN AND THE BIOSPHERE PROGRAM
DEPARTMENT OF STATE
WASHINGTON, D. C.

BY:

M. I. DYER
AND
D. A. CROSSLEY, JR.

DEPARTMENT OF ENTOMOLOGY
THE UNIVERSITY OF GEORGIA
ATHENS, GEORGIA 30602

Abstract. This report examines current and future problems for coupling remote sensing technology with ecological studies in temperate forest ecosystems. The discussions result from a two-and-one-half-day workshop at the University of Georgia in May 1985 and range widely. Needs for global, regional, and site-specific syntheses constitute the major theme. Summary statements and study approaches are given by representatives from four Biosphere Reserves: Coweeta Hydrologic Laboratory, H. J. Andrews Experimental Forest, Hubbard Brook Experimental Forest, and Great Smoky Mountains National Park. Computer models for managing site-specific information so it can be assembled for subsequent integration into regional descriptions are reviewed, and a discussion of a new generation of models to cope with hierarchical problems in ecology is presented. Three papers show, in varying detail, how such hierarchical arrangements can be used to link ecological information and remote sensing. The main conclusion emanating from the workshop is that new research and development involving both state variable and process information must be designed to increase the potential for utilizing remote sensing and to help measure ecological problems on both local and global scales. This new work should be based in analysis of dynamical aspects of ecosystem function so that a strong tie can be built back to higher order dynamics of regional and global problems. An important facet is learning how to deal with uncertainty in large ecological systems. A new emphasis on process-level research is urged so that in the future it will be possible to construct new and different ways to merge remote sensing and ecological studies.

CONTENTS

Page

Chapter 1. Introduction. The Workshop Setting - A Sense of Direction. M. I. Dyer and D. A. Crossley, Jr. 1

Chapter 2. Global and Regional Synthesis: Needs and Opportunities for a Hierarchy of Scales of Remote Sensing and Modeling. J. S. Olson 9

Chapter 3. Coweeta Hydrologic Laboratory Background and Synthesis. W. T. Swank and D. A. Crossley, Jr. 23

Chapter 4. Information on the H. J. Andrews Experimental Forest, Western Oregon Cascade Range. J. F. Franklin and R. A. Waring 33

Chapter 5. Hubbard Brook Experimental Forest Background and Synthesis. R. S. Pierce and T. G. Siccama 43

Chapter 6. Remote Sensing and Landscape Pattern in Great Smoky Mountains Biosphere Reserve, North Carolina and Tennessee. P. S. White and M. D. MacKenzie 52

Chapter 7. Computer Models of Terrestrial Ecosystems. H. H. Shugart and T. M. Smith 71

Chapter 8. Predicting Ecosystem Properties from Physical Data: A Case Study of Nested Moisture-Climatic Gradients Along the Appalachian Chain. J. Pastor and M. Huston 82

Chapter 9. North American Vegetation Patterns Observed with Meteorological Satellite Data. S. N. Goward, C. J. Tucker, and D. G. Dye 96

Chapter 10. Linkages in Hierarchical Models. D. L. Urban, R. V. O'Neill and H. H. Shugart 116

Chapter 11. Landscape Ecology: Spatial Data and Analytical Approaches. J. R. Krummel 125

Chapter 12. Summary: "The Present as the Key to the Future." M. I. Dyer and D. A. Crossley, Jr. 133

CHAPTER 1. INTRODUCTION: THE WORKSHOP SETTING-A SENSE OF DIRECTION

M. I. DYER

AND

D. A. CROSSLEY
Department of Entomology, University of Georgia, Athens, Georgia, 30602

With growing awareness of global problems caused by increasing human population levels and associated agricultural and industrial transformation of the earth's surface, scientists have had to refocus their approaches to describe these changes. No longer are traditional studies of point locations deemed sufficient to address problems of environmental change with global scale or consequence. Instead, there is a steady turn toward technological developments in the past decade which allow assessment of terrestrial events from remotely located sensors. The techniques are based in understanding how various parts of the electromagnetic spectrum are reflected or emitted from the surface of the earth and the ability to readily observe and measure these responses. Many research disciplines have taken great advantage of this relatively new technology: classification and determination of areal extent of land-use characteristics; accurate determination of bodies of water, including shore lines, location of land-water interfaces, and their fluctuations; and documentation of topographic features and variations across continents are but a few examples of the types of assessments that have resulted in dramatic changes in the way we consider our global environment. For example, one of the most dramatic presentations is the description of land cover and changes in green-leaf biomass for the whole continent of Africa over a 19-month period (Tucker et al. 1985). All of these studies have benefited from ground-level to high-flying aircraft to earth-orbiting satellite remote sensing studies.

For a variety of reasons the types of studies just referred to have concentrated on the definition of state variables. This, of course, is the first requisite in any scientific study: learn what is in one's environment and describe it. The second step, then, is to learn how these elements change. What type of change is exhibited by the object? How widespread is the change? How fast does it change? And, are there any discernible patterns or external connections to the change? If it is difficult in any way to determine the state variable configurations in the first place, it follows that it is immensely more daunting to determine the inherent processes and their transfer rates. Therefore, when we speak of global problems dealing with changing terrestrial and aquatic environments, we automatically turn to what we know about the state variables and then concentrate on their processes (Slobodkin 1984, Dyer and Crossley 1986). However, it is not immediately clear that it is possible to determine conditions of a state variable in two successive periods of time and ascribe to that variable cause and effect associated with changes in its state. Thus, in order to acquire information about large-system change it will become necessary to focus on events other than the state variable itself, and instead learn about processes that contribute to the changes we may perceive. This means that for vegetation change in terrestrial systems we have to focus on something other than greenness related to biomass. For some subjects, the use of remote sensing from any level may be relatively simple, but for most problems, the task may be next to impossible (see Botkin et al. 1984 for presentation of some problem areas). Nonetheless, new technologies, or new ways to use old information need to be fully explored before it can be said that we have the capabilities of developing a truly robust approach for detecting global change in the environment.

A recent report from the working group studying science and mission requirements for the Earth Observing System (EOS) (NASA 1984) recommends several projects which must begin soon in order to meet the deadlines of the 1990s being discussed for this system (see NASA 1984, Vol. 1, pages 49-51). The main reason for this development is an awareness of needs for what is termed an International Geosphere- Biosphere Program (NRC 1986). These publications point out that new efforts must be defined to accomplish the inter- and multi- or even transdisciplinary efforts needed to carry out this massive program. For instance, it is suggested that new data sets should be acquired to describe biophysical units, such as leaf area across continental areas, and ocean and inland water chlorophyll concentrations. To do this, it will be necessary to use present remote sensing systems and new systems to be launched on satellites late in this decade, or early in the next. However, before that can be done, a great deal of research must be designed in order to provide preliminary and final algorithms for these instruments, particularly the new ones. This means the initial research work must be spelled out for a variety of terrestrial and aquatic ecosystems and that follow-up work must be carried out for validation purposes. Coincidentally, much of this needed whole-system description and validation work is already being considered in selected areas of the United States through the National Science Foundation's Long-Term Ecological Research Program (LTER) (Callahan 1984) and through the Man and the Biosphere's (MAB) Biosphere Reserve Program in the United States (Dyer and Crossley 1986, Peine 1985) and some foreign countries. Projects in these programs must be scrutinized thoroughly to determine what state variables and processes being used to describe the function of these terrestrial and aquatic environments can be utilized in developing the necessary background for experiments leading up to the definitions for EOS. The working group (NASA 1984) asks that ecologists, hydrologists, geologists, oceanographers, data managers, computer scientists, and scientists and managers from other necessary disciplines be sufficiently linked to the engineering capabilities to make for an efficient and useful EOS. The most efficient way to accomplish this task is to ensure that there are well-designed projects at key areas which can address issues necessary for the EOS program. Further, communications among these scientists must be enhanced. A variety of training programs and workshops should be structured to bring this about.

Two of the most far-reaching reviews to emerge from the examination of global circumstances in recent years concern 'Global Habitability' and its related scientific initiatives (NASA 1984, NRC 1986). Five basic science elements have been identified for further intensive research: (1) the Global Energy Balance, (2) the Global Hydrological Cycles, (3) Biogeochemical Cycles, (4) Biological Productivity, and (5) Land Surface Assessments. The basic objective of new studies would be to enhance the study of the biosphere so we can understand fundamental principles underlying its existence and to monitor changes which might threaten it. Despite the fact a great deal is known about the biosphere, it is generally acknowledged that this information base is too fragmented to describe a global view. The NASA (1984) and NRC (1986) reports point out the necessity for assembling a strong synthetic base from which new studies can be launched, as well as calling for a variety of new studies to augment what is currently known. The combined view of the plan promoting development of engineering and science components of the EOS and the reviews about the land-related global habitability issues give focus to what ought to be accomplished in the next decade, both by NASA and other agencies which have a function in determining global change of the biosphere.

In 1984, we proposed to the MAB Consortium that a workshop be structured to initiate some of these discussions among scientists interested in these problems and those that are active in principal MAB Biosphere Reserve programs. On a trial basis three U.S. Department of Agriculture Forest Service sites and one U.S. Department of Interior National Park that have been designated Biosphere Reserves were chosen: Coweeta Hydrologic Laboratory, North Carolina; H. J. Andrews Experimental Forest, Oregon; Hubbard Brook Experimental Forest, New Hampshire; and Great Smoky Mountains National Park, Tennessee (Fig. 1).

We made visits to all Biosphere Reserves, or to representatives from those sites, before the workshop was held to hold discussions about information bases and specific studies at each of these Reserves which might lend themselves to the development of long-term analyses appropriate for coupling fundamental ecological work and potentials for remote sensing. At the same time, researchers interested in global, continental, and regional questions, as well as those interested in means of representing these data bases to one another, were contacted. These discussions focused on methods ecologists and remote sensing technical scientists and engineers must use to coordinate their efforts into a program of the future which will allow global assessment with maximum efficiency.

THE WORKSHOP FORMAT

In May 1985 a workshop to review current conditions at the four Biosphere Reserves and state-of-the-art approaches to utilizing ecological information for calibrating ecosystem information-remote sensing approaches was held in Athens, Georgia. Over two and a half days, presentations of current conditions and discussions of future needs were reviewed by the participants (Table 1).

The workshop outline is presented in Table 1; those attending and their affiliations are in Table 2. Participants agreed to discuss ideas pertinent to the theme of coupling remote sensing and ecological information in temperate forest ecosystems. Introductory comments about the overall needs and problems in dealing with spatial and temporal scale in ecological problems were followed by synopses of system character and pertinent information bases at the four Biosphere Reserves around which a central focus is being considered. These were followed by presentations on global problems, how to measure key parameters, and specifics about integrating the information bases with various modeling approaches.

ORNL-DWG 86-9607

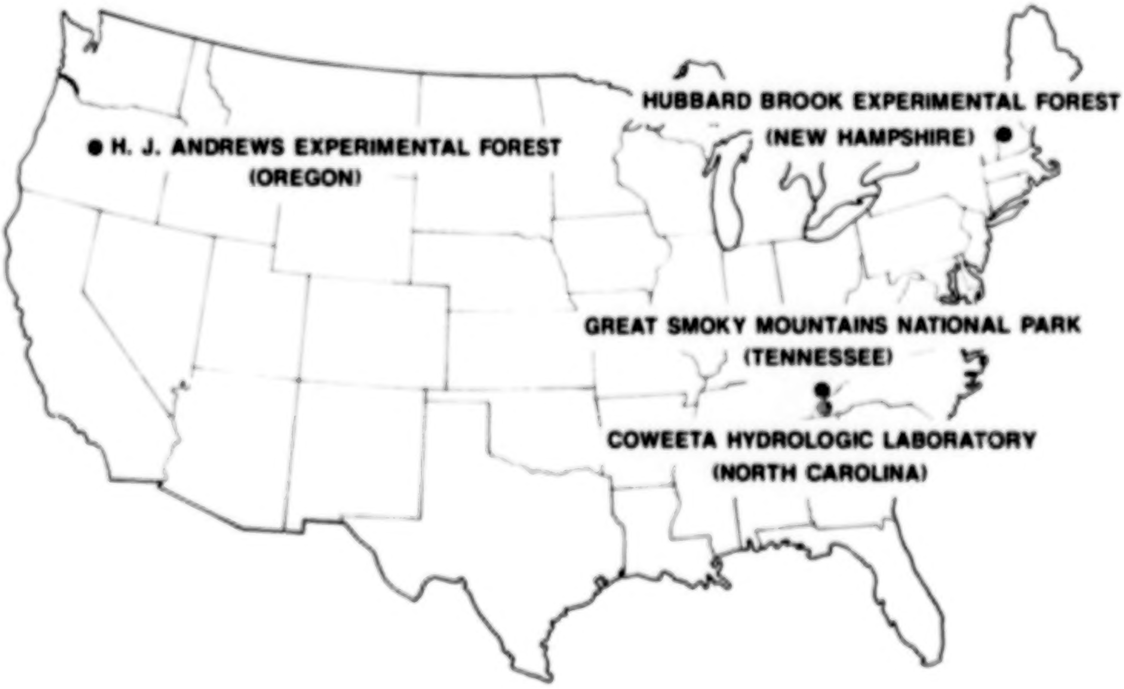

H. J. ANDREWS EXPERIMENTAL FOREST
(OREGON)
HUBBARD BROOK EXPERIMENTAL FOREST
(NEW HAMPSHIRE)
GREAT SMOKY MOUNTAINS NATIONAL PARK
(TENNESSEE)
COWEETA HYDROLOGIC LABORATORY
(NORTH CAROLINA)

Fig. 1. Location of four U.S. Biosphere Reserves that are focussed upon in this report.

BEST COPY AVAILABLE

Table 1. Abbreviated agenda for workshop held at the University of Georgia, May 15-17, 1985

Research Workshop: Man and the Biosphere.
Coupling of Ecological Studies on Three U.S. Forest Service
Research Sites with Remote Sensing Studies
University of Georgia
Athens, Georgia

Wednesday, May 15, 1986

08:30	Opening remarks	D. A. Crossley, Jr.
08:35	Workshop goals and charge	M. I. Dyer
08:45	Global and regional synthesis needs	J. S. Olson
09:15	Application of hierarchy theory in developing an ecology-remote sensing paradigm	H. H. Shugart and D. L. Urban
10:15	Synthesis reports: Coweeta Hydrologic Laboratory	D. A. Crossley, Jr., W. T. Swank, and J. B. Waide
10:45	Synthesis reports: H. J. Andrews Experimental Forest	J. S. Franklin and R. H. Waring
11:15	Synthesis reports: Hubbard Brook Experimental Forest	R. S. Pierce and T. G. Siccama
13:00	The use of global models in determining vegetation patterns	W. R. Emanuel
13:20	The potential of AVHRR for determination of forested ecosystem productivity	C. J. Tucker
13:40	Determination of landscape vegetation relations in Great Smoky Mountains National Park through remote sensing	M. D. MacKenzie and P. S. White
14:00	Use of remote sensing in large-scale ecological studies	D. B. Botkin
14:20	Leaf area of a coniferous forest estimated with Thematic Mapper	S. W. Running
15:10	Application of fractals for the analysis of landscape pattern	G. Sugihara
15:30	Quantifying landscape pattern: Analysis of land cover-land use data	J. R. Krummel
15:50	Use of mosaic simulators in natural forested landscapes	H. H. Shugart
16:10	Comparative ecosystem properties along the Appalachian chain	J. J. Pastor and M. A. Huston
16:30	Wrap-up; discussion of plans for Thursday workshops	

Thursday, May 16, 1985
Workshops in designated meeting rooms, 08:30-11:30; 03:30-16:30

Friday, May 17, 1985
Summary reports of workshop group representatives, 08:30-11:30

Table 2. List of participants at Athens Workshop

Research Workshop: Man and the Biosphere.
Coupling of Ecological Studies on Three USDA/FS
Research Sites with Remote Sensing Studies
University of Georgia
Athens, Georgia
May 15-17, 1985

W. H. Banzhaf,	George Banzhaf and Company, Milwaukee, Wisconsin
C. S. Bledsoe,	University of Washington, Seattle
D. B. Botkin,	University of California, Santa Barbara
E. O. Box,	University of Georgia, Athens
W. G. Cibula,	NASA, Mississippi
D. A. Crossley, Jr.,	University of Georgia, Athens
M. I. Dyer,	ORNL, Oak Ridge, Tennessee
W. R. Emanuel,	ORNL, Oak Ridge, Tennessee
J. F. Franklin,	USDA/FS, Corvallis, Oregon
J. R. Gosz	NSF, Washington, DC
M. A. Huston,	ORNL, Oak Ridge, Tennessee
D. A. Kovacic,	University of Georgia, Athens
J. S. Olson,	ORNL, Oak Ridge, Tennessee
W. S. Osburn,	DOE, Germantown, Maryland
M. D. MacKenzie,	University of Tennessee, Knoxville
R. S. Pierce,	USDA/FS, Durham, New Hampshire
S. W. Running,	University of Montana, Missoula
H. H. Shugart,	University of Virginia, Charlottesville
T. G. Siccama,	Yale University, New Haven, Connecticut
G. Sugihara,	ORNL, Oak Ridge, Tennessee
C. J. Tucker,	NASA, Goddard Space Center, Greenbelt, Maryland
R. H. Waring,	Oregon State University, Corvallis
D. E. Wickland,	NASA, Washington, DC

On day two, three subject groups were defined in which specific issues were discussed about fundamental ecological problems, current and future monitoring technology, and problems and approaches to coupling remote sensing and ecological projects. On the last day the entire group reassembled to discuss the various subjects. Several papers representing important discussion topics from the workshop have been prepared and are presented in this volume. In our concluding remarks we, the editors, have attempted to summarize topics that were discussed, and not otherwise reported upon. We end with a series of recommendations about future courses of action.

ACKNOWLEDGMENTS

Many have helped develop this project. We owe thanks to the workshop participants and those that prepared the final reports published here. Special thanks go to Dr. Roger E. Soles, Executive Director, U.S. Man and the Biosphere Program for implementing the project; to Ms. Polly Casale for her efforts in organizing the manuscript; to Ms. Polly Henry for preparing the manuscript; to Ms. Phylis Rubin and others of the U.S. MAB offices for helping with the publication process; and to P. F. Ffolliott, Chairman, W. H. Banzaf, C. S. Bledsoe, H. A. Mooney, and W. T. Swank, all of the U.S. MAB-2 Directorate on Temperate Forests, for their advice. This study has been funded by the U.S. Man and the Biosphere Program, Grant No. 1753-400525, to the University of Georgia.

LITERATURE CITED

Botkin, D. B., J. E. Estes, R. M. MacDonald, and M. B. Wilson. 1984. Studying the earth's vegetation from space. BioScience 34:508-514.

Callahan, J. T. 1984. Long-term ecological research. BioScience 34:363-367.

Dyer, M. I., and D. A. Crossley, Jr. 1986. The utilization of whole ecosystem data and models to calibrate remote sensing information. Pages 000-000 in A. A. Orio and D. B. Botkin (editors) The Science of the Total Environment, from the conference, Man's Role in Changing the Global Environment, Venice, Italy, October 21-25, 1985. Elsevier Publishing Company, Oxford.

NASA. 1984. Earth observing system. Volume I, Part I Working Group Report. TM-86129 NASA/Goddard Space Flight Center, Greenbelt, Maryland 20771.

National Research Council. 1986. Global Change in the Geosphere-Biosphere: Initial Priorities for an IGBP. National Academy Press, Washington, D. C.

Peine, J. E. (editor). 1985. Proceedings of the Conference on the Management of Biosphere Reserves, November 27-29, 1984, Great Smoky Mountains National Park, Gatlinburg, Tennessee. U.S. Department of the Interior, National Park Service, Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, Tennessee.

Slobodkin, L. B. 1984. Toward a global perspective BioScience 34:484-485.

Tucker, C. J., J. R. G. Townshend, and T. E. Goff. 1985. African land-cover classification using satellite data. Science 227:369-375.

CHAPTER 2. GLOBAL AND REGIONAL SYNTHESIS: NEEDS AND OPPORTUNITIES FOR A HIERARCHY OF SCALES OF REMOTE SENSING AND MODELING

JERRY S. OLSON
Global Pattern Associates, Box 361A, Route 2,
Lenoir City, Tennessee 37771

Abstract. Since early years of systems ecology and the International Biological Program (IBP), a recurring challenge has been to cope with the vastly contrasting scales of the biosphere's patterns. The search has been built upon from the experiences on relatively few intensively researched grounds, like on the few Biosphere Reserves discussed here. Understanding the geochemical balance of the atmosphere and lithosphere must address the unbalanced carbon budgets in whole regions of the biosphere. This demands new sources of information and models on scales ranging from a hectare or kilometer to global zones of major ecosystem complexes. Relevant techniques of landscape scanning need to be compared and combined. Data resolution (pixels) spans a few m [aircraft; System Probatoire d' Observation de la Terre, or SPOT (Welch 1985)], 30 or 80 m (LANDSAT Thematic Mapper, TM; Multispectral Scanner, MSS), and 1 to many km (Advanced Very High Resolution Radiometer, AVHRR). An example using the Great Smoky Mountains National Park shows nested arrays of early (1972) MSS landscape pattern that are significantly related to ecosystem contrasts between spruce-fir on summits and various broadleaved forests and scrub (plus or minus pine or hemlock) elsewhere.

INTRODUCTION

A cartoon (Fig. 1) shows a research team standing on the west side of the Cascade Mountains in the Pacific Northwest intensely mining details from the 'mother lode' of the H. J. Andrews Experimental Forest. Out in the sparsely inhabited desert I stand, wondering how it is going to be until Long-Term Ecological Research areas (LTERs) and Biosphere Reserves can be used for creating and testing coherent models of our global ecosystem or its major representative landscape complexes (Olson et al. 1983, 1986; Olson and Watts 1983).

Somewhere in the rarified air of the summits of science's present capability is a place where we can look both ways--downward (west) to take full advantage of local insight and outward (east) toward a global view. I here use 'global' first in the commonest sense, meaning worldwide, but also in a second, more abstract meaning for total or generic: to cover the essence of a whole class of complex problems instead of particular cases in isolation.

I note some general needs for global and regional research and the paradoxical difficulty of finding a common ground in regional systems of intermediate scale, all of which offer a transition between the very large and small. From such a middle ground we should like to reach one hand toward the

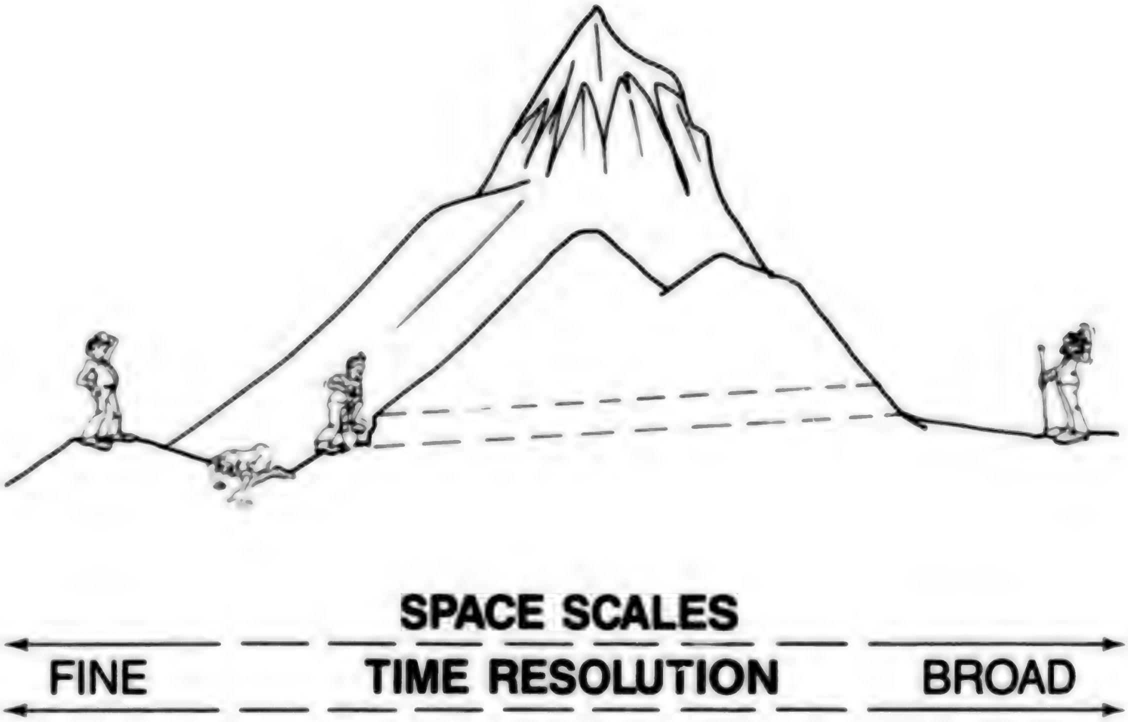


Fig. 1. Challenge! Uniting specialized research 'mined' on local experimental areas (e.g., H. J. Andrews Experimental Forest on west slopes of Cascade mountain range) and regional or global vistas of the world ecosystem, or ecosystems in general. Can a tunnel connecting both kinds of research be bored through the mountain barrier from both sides and meet in the middle? Alternatively, what would it take to create a science of landscape ecology to work from intermediate scales toward both finer and broader resolutions of a new, multi-scale world view?

BEST COPY AVAILABLE

subsystem specialists, and another toward global synthesis. First, the worldwide scale and the carbon cycle whose understanding requires estimates of how all major ecosystems collectively exchange carbon with the atmosphere. Second, intensive studies of contrasting ecosystems quantify the meaning of parameters defining the rates of flux of energy and matter through stands of diverse landscapes.

Lastly, I turn to a nesting of intermediate spatial scales to show how we can resolve the proportions of ecosystem and site types within a landscape with the aid of remote sensing [the Great Smoky Mountains (GRSM) is the example of multispectral scanning]. By using extreme scales of remote sensing, one can clarify the nature of ecosystem complexes. For the GRSM these are resolved into separate patches with aid of high resolution sensors and aircraft. Such patches become merged as more or less regular 'fine texture' when we view communities and landscapes together within major patterns and processes for which we can sum parameters over whole regions to a planetary scale.

GENERAL CHALLENGES FOR GLOBAL AND REGIONAL SYNTHESIS

The Need to Transcend Scales of Space and Time

This Athens meeting of Man and the Biosphere and Fig. 1 thus remind me of a parable I discussed at Brussels in 1969 (see Olson 1971, pages 236, 255). Engineers are drilling a tunnel from two sides of a great mountain range, to meet in the middle; no small task. Similarly, it will require meticulous surveying and lots of hard work to assure that the reductionists of science and those with global visions can get together, so that the middle grounds of landscape and regional ecosystem science can be developed. As in the parable, "A better survey of the ecosystem itself may be needed to assure the joining of regionally and mechanistically oriented specialists. The landscape survey, in both cases, may have to depend on mathematics to join their pieces..."

The Use of New Approaches on All Scales

Since 1969 we, the public, have been awed by two vast proliferations in environmental science (1) developing awareness of how humans impact the biosphere on regional and planetary scales and (2) an outpouring of technical data about the Earth's changeable scenery, which offers an opportunity to measure and define the impacts. Yet, science still seems barely on the threshold of using the raw information for critical evaluation of environmental change on either regional or global scales. Crossing that threshold must show us how well satellites can help to improve not only the descriptive surveys, but equally important, the comprehension of what its patterns of change will mean for future generations: a Rosetta Stone for deciphering a new language of the Earth.

GLOBAL SYNTHESIS FOR CYCLING OF CARBON AND OTHER ELEMENTS

The global geochemical cycle of carbon has long operated to recharge the atmosphere's balance of oxygen and carbon dioxide so life, as recorded in the fossil record, could continue and evolve. Yet the quantitative balance of carbon compounds has been changing on many scales of time as well as space. For at least 3.5 billion years of earth's history most of the carbon fixed from the atmosphere (equations 1 and 2) has been returned to the air, after geologically brief delays in the form of organic compounds before their decomposition:

surplus production = gross primary production
- respiration of green parts of plants; (1)

net primary production = surplus production
- respiration of other plant parts; (2)

plant mass change = net primary primary production
- loss by death or shedding of parts
- harvest or other removals; (3)

Change of live biomass (eq. 3) has fluctuated, perhaps becoming negative rather briefly when major episodes of extinction came about for whatever disturbances. A sustained buildup of woody vegetation followed the evolution of vascular plants in late Silurian and Devonian times. The Cenozoic Era, the last 60 million years, has probably had a net decline in plant biomass as grasslands, deserts, and then tundra species evolved to spread over large land areas (Olson 1985). Within the last million years of the Pleistocene, forests have been pressed back episodically, not only by repeated glacial readvances, but by aridity in cold and hot deserts and semiarid belts where grasslands alternate with scrub and low trees.

Through most of this time, in wetlands, dead carbon in peat or dispersed in other sediment may have been laid down, at rates up to a billion metric tons of carbon per year in recent centuries, as humans hastened erosion of humus and increased development of reservoirs. Some of this deposited carbon is recycled to air before and during consolidation of loose sediment into rocks, a net withdrawal of carbon dioxide into sediments at a rate averaging 0.04 to 0.06 billion metric tons of C per year (Olson et al. 1985). This difference of almost a billion tons of C going into what we call 'subfossil' carbon, but not lasting through the rock cycle into fossil carbon of consolidated rocks may currently be far from balance in the global geochemical cycle (Olson et al. 1985).

Indeed, this temporary imbalance of excess deposition may be an important part of the answer resolving questions by geophysicists and ecologists about how the ocean can absorb the excess carbon dioxide being poured into the air by the combination of burning old sedimentary carbon (fossil fuel) and reducing the biosphere's storage of organic carbon in plants and humus. Everyone now realizes the striking increases of atmospheric carbon dioxide over the past and next century, but a state-of-the-art review of this subject (Trabalka 1985) suggests that that increase would have been much greater if there were not important sinks besides the ocean to help dispose of the combined fossil and nonfossil carbon being released to the atmosphere.

I do not believe nor intend to infer that the net imbalance of the biosphere's carbon is as great as the 5 billion tons per year that are currently recycled to the atmosphere from the fossil carbon laid down during previous geologic eras. But even 1 or 2 billion tons per year is a huge part of the overall change to be left unresolved in the global equation, for carbon cycling, for its implications on climatic history, and for impacts of altered carbon dioxide and climate. The functioning of the biosphere as a resource for its own life support and ours may be highly dependent on this carbon reservoir, which is extremely difficult to measure with precision and reliability.

REVIEW OF SUBSYSTEM STUDIES OF PROCESS

For resolving some of the larger world issues about carbon cycling, it is essential to alternate from the foregoing point about looking from the whole globe downward to a finer analysis of components and subsystems, so we may build back upward to a more complete holistic view. A second reason for continuing the typical scientific preoccupation with small pieces of the larger problem is that most effects or impacts of climatic change and enriched carbon dioxide affecting production rates will be different from place to place. It will vary according its own history and boundary conditions, including genetic capabilities of organisms that became preconditioned by evolution and acclimation.

Rates and Indexes of Primary Production

On all scales, from the green leaf or its chloroplast to the whole vegetation mantle's absorption of carbon dioxide, fixation of solar energy (very limited wavelengths of red or blue) is the mainspring which drives the pulse of our planet's life (Olson et al. 1985). Photosynthesis, or gross primary production of organic compounds, supports all food chains and is finely researched at the levels of biochemistry and ecophysiology. Chapter 9 by Goward et al. shows how the greenness of North America or the whole biosphere can be sensed routinely by comparing the ratio of difference between red and infrared reflectance of vegetation divided by the sum of the same reflectances.

Gross primary production becomes discounted at three or more levels that represent the negative terms in equations (1) to (3), respectively. After a respiratory income tax taken by the foliage itself, surplus production (equation 1) is left for the rest of the plant, or global vegetation (Olson 1975). Second, respiration of nongreen parts is deducted, like a kind of property tax (Olson 1964), more or less proportional to the various fractions of rapidly and slowly metabolizing tissues; their mass per unit area can be very large in old-growth forests like those available in the GRSM. The rate of net primary production (equation 2) is remainder, after both of these taxes are deducted, but it is nevertheless greater than biomass change (equation 3). From positive increments of growth are deducted consumption by animals and continuous or episodic death and fall of individuals or their parts. Net increments of dry matter are sometimes treated as if they were unbiased estimators of production rates, when in fact they are at best lower bounds if these deductions are omitted for lack of information on the following:

animal mass change = consumption of food - ejecta
- animal respiration
- loss by death or shedding of parts
- harvest or emigration (4)

change of detritus = income (from organisms or imports)
- respiration by decomposers
- exports (downhill, downstream, fire) (5)

The inherent difficulty of estimating belowground parts of plants and their turnover rates adds to the problem of estimating local and global fluxes of primary and secondary production.

Release of Organic Energy, Carbon Dioxide, and Mineral Nutrients

Sometimes fire kills suddenly and burns residues instead of leaving them for slow microbial oxidation, recycling in a few hours the inputs and accumulations of many years (Olson 1981). Plant mass (phytomass) and detritus (necromass) invite consumption through animal food chains. Plants, debris, and animals temporarily store nutrient elements besides carbon, until these are released by decomposition and become available for catalyzing new rounds of primary production (of plants) and secondary production (of consumers and decomposers). We need to quantify key state variables and their mathematical relations to fluxes of income and loss of significant elements in order to complete the analysis of the cycling of organic carbon (to the atmosphere as carbon dioxide or methane) and of some of the critical nutrient elements.

In GRSM (Fig. 2), field research by Whittaker (1956, 1966), Shanks and Olson (1961), Whittaker, et al. (1963), and Becking and Olson (1978) has explored how patterns of primary and secondary producers and rates of decomposition of litter vary with the climatic gradients. Classic contrasts occur (Olson 1971) between sites of unusually high production and biomass (e.g., cove hardwood and hemlock forests) vs. open stands of pine or oak with heath understories (locally dense heath scrub on the driest ridges with fire history). We should like to take advantage of remote sensing data (see below), first to improve the mapping of sites of extremely high and low biomass and intermediate members of the continuum. Then we need to count pixels as a step toward evaluating the extent or importance of all major parts of the soil/substrate catenas which store and replenish fluxes of water and nutrient, in order to sum over the whole mountain's productivity, decomposition rate, and net energy flow.

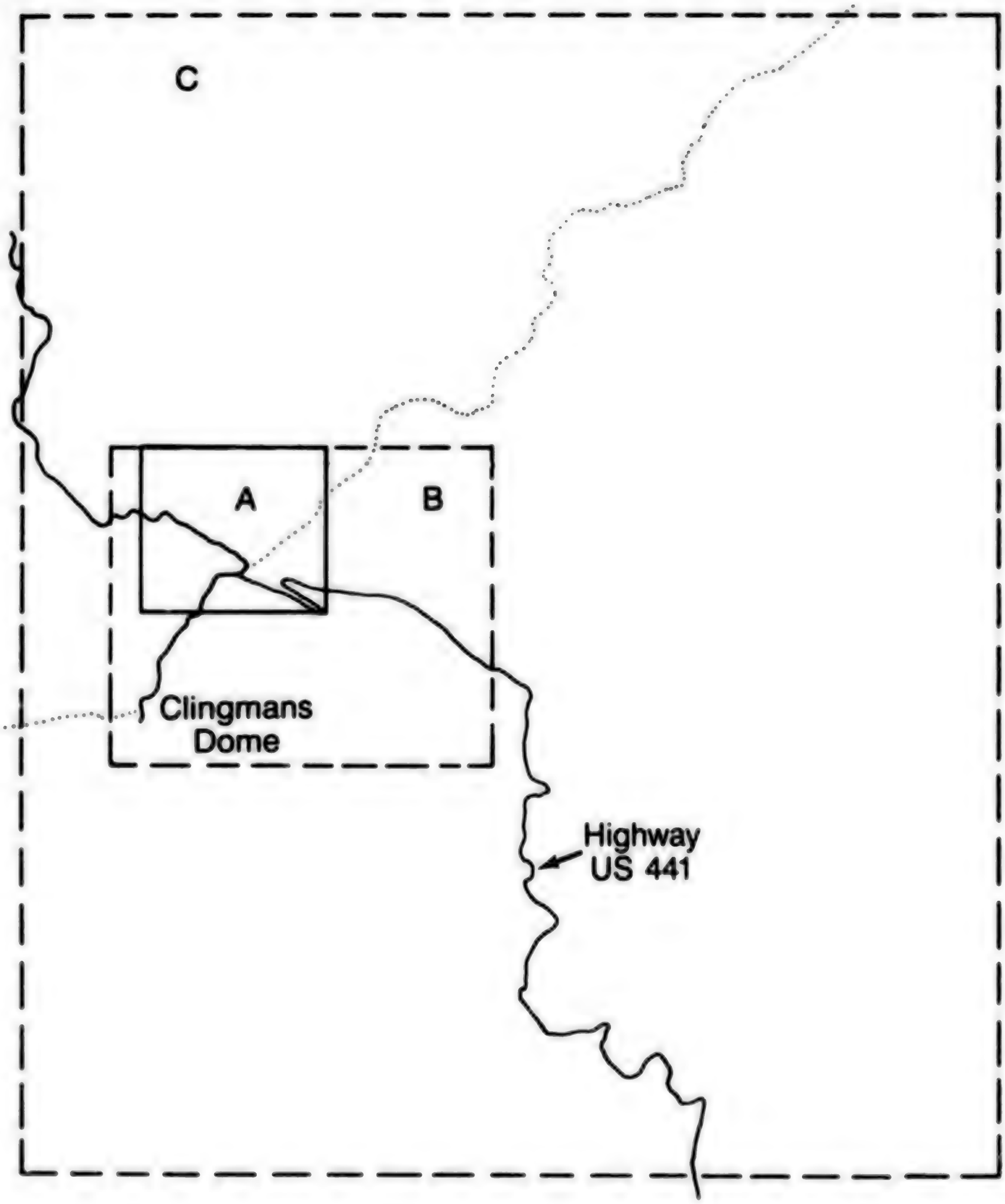


Fig. 2. Locations within Great Smoky Mountains National Park, Tennessee showing locations of remote sensing arrays (areas A, B, C; see Fig. 3) nested around the Clingmans Dome quadrangle (1:24,000) within the Knoxville quadrangle (1:250,000).

BEST COPY AVAILABLE

Ecosystem Fluxes and Micrometeorological Processes

That small fraction of the total radiant energy flow which contributes to equations (1) through (5) needs to be related to the larger net radiant energy income (direct and diffuse short-wave downward flux) and loss (upward flux of short wave and thermal radiation; latent heat flux mostly as evaporation; sensible heat exchange over the cycles of the day or year). Only by combining the ecosystem analysis of energy and nutrients with the micrometeorology of complex landscape surfaces can we interpret the processes affecting the large, important areas of continental surfaces, especially those irregular terrains which do not have the convenient uniformity of flat areas, such as man-made topography, grasslands, or crops. The data have to be interpreted in terms of local processes and physical or biological disciplines in order to be global in the second sense emphasizing generic principles. Further, the results have to be handled at regional and worldwide scales so we do not have to wait inordinately to get detailed intensive research in every corner of the earth.

ANALYZING LANDSCAPE PATTERNS BY REMOTE SENSING

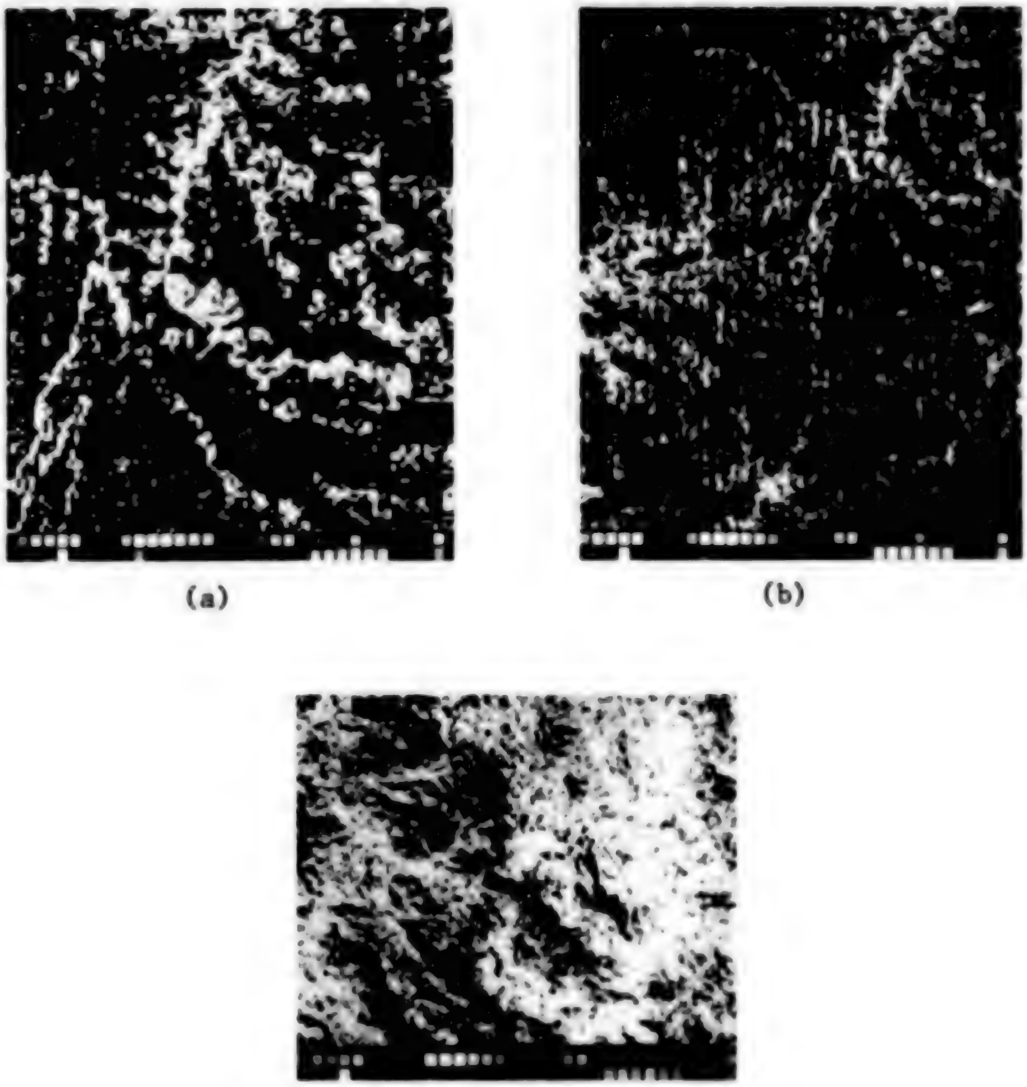
Methods of Composite Arrays

The examples in Figs. 2 and 3 shows three scales of sampling the Multispectral Scanner (MSS). The scene from the GRSM is one of the first obtained by LANDSAT 1 on a nearly clear day in October 1972 (but with ground fog in a few valleys). After some early analyses of this scene, results shown in Figs. 3a, 3b, and 3c were based on an analysis I have made with help of the Space Sciences Laboratory at The University of California, Berkeley. Techniques are summarized by Colwell (1978).

Three visible and one near-infrared band of the MSS were used in a maximum likelihood classification of vegetation signatures emerging in a season of autumn foliage colors. A nesting of images was made simply by deleting alternate rows and columns, not by averaging the small groups of values for picture elements (pixels) in the larger area images. We still need to explore optimal approaches to smoothing out variability, perhaps in the way White and MacKenzie (Chapter 6) suggest.

Results of Nested Images

Figs. 3a, 3b, and 3c were assigned to colors based mainly on the ratio of the near-infrared and red reflectance. On Fig. 3a the pixels of about 80 m clearly separate the false-color red images of oak and other deciduous broadleaved trees, mainly on the North Carolina (lower right) side of the state line ridge representing the boundary with Tennessee. Yellow includes not only northern hardwoods and other mesophytic broadleaved trees (sometimes with a mixture of rhododendron or an understory of conifers, but also some of the secondary sapling thickets along the winding transmountain highway (U.S. 441; sometimes showing white where widened in parking lots, as at Newfound Gap). Various blue shades clearly



(a)

(b)

(c)

Fig. 3. Three scales of Multi-spectral Scanner (MSS) imagery with 80-m picture elements (pixels), along the Great Smoky Mountain crest, state boundary of Tennessee and North Carolina (see Fig. 2). (a) All pixels; near U.S. 441 crossing of transmountain highway at Newfound Gap. (b) Alternate rows and columns; summit belt of spruce-fir forest from Clingmans Dome area. (c) Sparser sampling from Ridge and Valley province landscape encompassing large proportion of GRSM.

correspond to the forests of red spruce (*Picea rubens*) and endemic Fraser fir (*Abies fraseri*, approximate counterpart of the more northern *Abies balsamea*). These conifers are limited mostly to altitudes above 1400 m, and are commonly interspersed with yellow birch (*Betula alleghaniensis* or *B. lutea*) or locally alternating with nearly pure beech (*Fagus grandifolia*).

Fig. 3b shows almost all of Appalachia's most southwesterly outlier of this cool conifer forest in blue or dark green, clearly extending south and west slightly past the highest peak of the Park, Clingmans Dome (Fig. 2). On the upper left are the conifer-topped 'lead' ridges of Mt. LeConte, where dark conifers are infrequently interrupted by patchy hardwoods (e.g., pin cherry, *Prunus pensylvanica*, on disturbed areas, as well as yellow birch) and by a sinuous rocky trail descending to the corner of the image. Radiating from the south central edge of Fig. 3b are the branches of Deep Creek, whose lower slopes have mesic forests (yellow), where productivity presumably is enhanced by reserves of moisture and nutrients which are input to these forests after downhill flow from the upper slopes. Here green signatures apparently include hemlock (*Tsuga canadensis*) on such moist sites and midslopes, and pine on drier slopes, which commonly have evidence of long histories of burning.

Fig. 3c covers a wider area (most of the southwest quadrant of LANDSAT scene 35 of row 18) at the expense of thinner sampling of detail. For reconnaisance, made before the finer tuning of landscape classes of Figs. 3a and 3b, it included a somewhat more granular coverage of the central Smokies in the left center. Spruce-fir (and the waters of Fontana Lake in the lower left) are almost black, reflecting least infrared radiation. Yellow covers a wider span of mixed and intermediate reflectance. Along with green [Virginia pine (*Pinus virginianus*) and shortleaf pine (*P. echinata*)], it dominates much of the Ridge and Valley Province shown north of the Smokies (Blue Ridge Physiographic Province). White areas that did not correspond to any of the classified wild landscapes probably represent agricultural and other disturbed cover (east of Sevierville, Tennessee). Red still corresponds with deciduous forest, but a more limited range of (high) reflectance of near infrared than in the classification in Figs. 3a and 3b, mostly in old growth or regrown forests of the bolder, older Appalachians further south.

At all three scales of Fig. 3, at the broader continental scale illustrated by Goward et al. (Chapter 9) and at the finer scales of aircraft Simulated Thematic Mapper (TSM) imagery discussed by White and MacKenzie (Chapter 6), we are offered arrays of landscape pattern that challenge us to interpret what vegetation, terrain and ecosystem properties correspond to the varied spectral signatures. Further, the results to date challenge us to determine how well we can quantify the fluxes of energy and organic mass (equations 1-5) that presumably vary in a systematic way for local sites, regions, and global zones that differ in these optical properties.

A Nested Array of Large-Scale Models

The regional requirements for modeling will require explicit mathematical form and parameter values for transfer rates among organisms, natural resources, commodities for human communities, or between the more and less productive parts of the ensemble of landscape units (Urban et al., Chapter 10) (Fig. 4a). Global modeling requires summing over the whole frequency distribution of the regional ensemble, e.g., in the exchange between the biosphere as a whole and the atmosphere, hydrosphere, and lithosphere.

When goals developed for regional or global programs are foreseen as part of the long-range objectives at the strategic level of a modeling paradigm, then models representing forest stand populations, or organismal components can be scrutinized on scales larger than those considered originally. Many models (like JABOWA and FORET) are not just replicates of populations in which many species or individuals of many size classes are kept separately in rather massive computer memories (Fig. 4b). Rather, the 'populations' of landscape units within the larger ensemble of Fig. 4a become the main study. Similarly, ecophysiological models which attempt to be global in the sense of treating biophysical principles in functional parts of an individual producing plant, animal, or soil horizon (Fig. 4b) can eventually approach worldwide coverage in degrees. For carbon cycling this can be developed by proportionate weighted averaging among the biochemically distinct categories of plants and functionally contrasting groups of consumers and decomposers, which together regulate exchange between the whole biosphere and atmosphere (Fig. 4c).

CONCLUSIONS

To continue my earlier quotation (Olson 1971, page 255), "We cannot bore a tunnel through a mountain by starting in the middle and working in both directions. However, IBP and any subsequent programmes on human environment can include one feasible strategy for ecosystem research which starts at an intermediate degree of size and detail (Fig. 3). This helps to focus everyone's attention sharply on an ecosystem the size of a stand or small watershed. At least periodically, if not constantly, the process-oriented specialist can see where his own results will have significance for this system, beyond their importance for his own sub-discipline (Fig. 4). Also the geochemist, or resource manager responsible for large regions, can cite balanced, but localized case studies for seeing principles, general magnitudes, interrelations and controls which apply more widely but which could not be investigated in equal detail over the whole earth..."

In the years since the foregoing was published, satellite imagery has begun to provide the data bases for just such a science of landscapes, for catchments larger than mere headwaters, and for a hierarchy of regions or zones that can be compared and combined in a worldview that is global in both senses of that word. I conclude: (1) that the seemingly visionary plan of boring a tunnel toward both sides of the mountain from the inside (the intermediate scales) has become feasible in a way we could only dream for in 1969; (2) the challenge of global problems and the opportunities for data to address them can come together, like the tunnelers and then the travelers from both sides of our scientific tradition; (3) on the global scale which cannot be evaded for carbon cycling and climate problems, the equations (1) to (3) on primary production can become quantified in

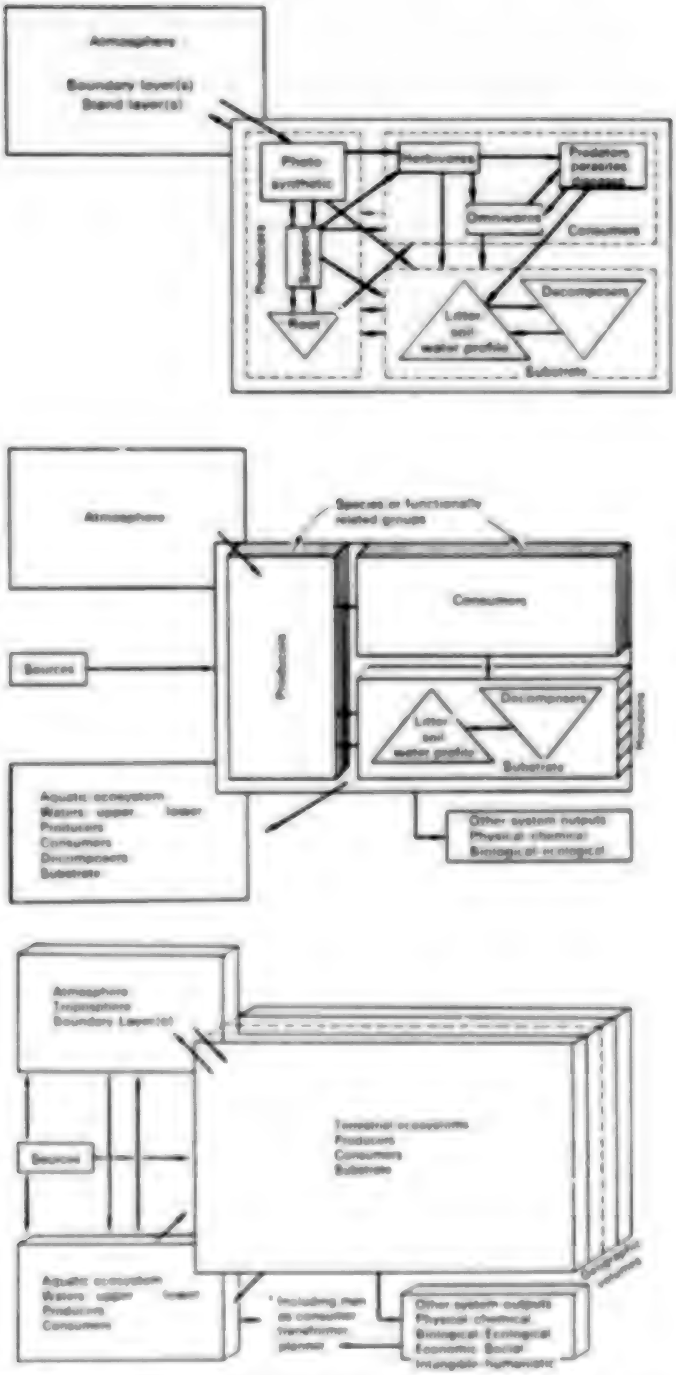


Fig. 4. Three kinds of system resolution, appropriate for mathematical modeling at different scales. (a) Producing and storage components of carbon in an ecosystem, to be used or elaborated for ecophysiological models of major species or functional group(s). (b) Multiple taxa or population models for producers (e.g., FORET) and consumers, with horizon levels for detritus and substrate for typical landscape element or ensemble. (c) Ensembles of stand-site systems, extended over a spatial grid or ordered array landscape or regional conditions, summing up to essential conditions or a region or global system. After Figs. 2, 3, and 4 of Olson 1971.

intensive research sites, and become extended for all spatial scales; (4) much remains to be done for understanding how much delay is entailed before animals and microorganisms recycle the plant carbon back to the atmosphere, and intensive subsystem studies are essential for completing the ecosystem paradigm in the most contrasting and interesting climates and microclimates of the world; and (5) the landscape patterns which are revealed at any of the spatial scales of remote sensing challenge us to decipher the meaning of arrays combining the best and worst sites of any given region, in addition to helping our bookkeeping to add up the areas and productivities of the component landscapes of any region.

Toward this end, we may work from models of middle-sized systems toward fine analysis of their components and synthesis of their global meanings, quite unlike our 'tunneling parable' (Fig. 1). Doing so will require organized data hitherto beyond our reach, but now becoming available hrough regional ensembles (Figs. 2-4a). From these, reaching downward as well as upward (Figs. 4a,b,c) will help new syntheses make fuller use of work on all scales of space and time.

ACKNOWLEDGMENTS

The remote sensing test was begun for U.S. National Science Foundation sponsored research on "Terrestrial Ecosystems, Climate, and the Global Carbon Cycle" (DEB77-26722) while in the Environmental Sciences Division of Oak Ridge National Laboratory. Support has been provided by the U.S. National Aeronautics and Space Administration's Thematic Mapper Working Group from the Illinois Natural History Survey Botany Department, through NASA's Goddard Space Flight Center, Greenbelt, Maryland. The University of California, Berkeley, Space Sciences Laboratory helped prepare Fig. 3. M. I. Dyer and D. A. Crossley and others aided the report preparation for the U.S. contribution to Man and the Biosphere (MAB), with support from NSF, the USDA Forest Service, and NASA. I also thank participants in the Athens, Georgia, workshop and Institute of Ecology staff for stimulating ideas over many years.

LITERATURE CITED

Becking, R. W., and J. S. Olson. 1978. Remeasurement of permanent vegetation plots in Great Smoky Mountains National Park, Tennessee, USA, and the implications of climatic changes on vegetation. ORNL/TM-6083, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Colwell, R. N. 1978. Interpretability of vegetation resources on various image types acquired from earth-orbiting spacecraft. Journal of Applied Photogrammetric Engineering 4:107-117.

Olson, J. S. 1964. Gross and net production of terrestrial vegetation. Journal of Ecology 52, Supplement:99-118. (Jubilee lecture, British Ecological Society).

Olson, J. S. 1971. Primary productivity: Temperate forest, especially American deciduous types. Pages 235-258 in UNESCO. Productivity of Forest Ecosystems, Proceedings Brussels Symposium 1979. (Ecology and Conservation 4.).

Olson, J. S. 1975. Productivity of world ecosystems. Pages 33-43 in D. E. Reichle, J. F. Franklin, and D. W. Goodall (editors), Productivity of World Ecosystems. National Academy of Science, Washington, D.C.

Olson, J. S. 1981. Carbon balance in relation to fire regimes. Pages 327-378 in H. A. Mooney, T. M. Bonnickesn, N. L. Christensen, J. E. Lotan, and W. A. Reiners (editors), Fire Regimes and Ecosystem Properties (MAP-SCOPE Workshop), USDA Forest Service General Technical Report WO-26, Washington, D.C.

Olson, J. S. 1985. Cenozoic fluctuations in the biotic parts of the global carbon cycle. Pages 377-396 in E. T. Sundquist and W. S. Broecker (editors), The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. American Geophysical Union Monograph 32, American Geophysical Union, Washington, D.C.

Olson, J. S., J. A. Watts, and L. J. Allison. 1983. Carbon in live vegetation of major world ecosystems. ORNL-5862. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Olson, J. S., and J. A. Watts. 1983. Major world ecosystem complexes. (Addendum to: Olson, Watts, and Allison 1983).

Olson, J. S., R. M. Garrels, R. A. Berner, T. V. Armentano, M. I. Dyer, and D. H. Yaalon. 1985. The natural carbon cycle. Chapter 8 in J. R. Trabalka (editor), Atmospheric Carbon Dioxide and the Global Cycle of Carbon. U.S. Department of Energy, Technical Information Center, Oak Ridge, Tennessee.

Shanks, R. E., and J. S. Olson. 1961. First-year breakdown of leaf litter in Southern Appalachian forests. Science 134:194-195.

Trabalka, J. R. (Editor). 1985. Atmospheric Carbon Dioxide and the Global Cycle of Carbon. U.S. Department of Energy, Technical Information Center, Oak Ridge, Tennessee.

Welch, R. 1985. Cartographic potential of SPOT image data. Programmetric Engineering and Remote Sensing 51:1085-1091.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103-121.

Whittaker, R. H., N. Cohen, and J. S. Olson. 1963. Net production relations of the three tree species at Oak Ridge, Tennessee. Ecology 44:806-810.

CHAPTER 3. COWEETA HYDROLOGIC LABORATORY BACKGROUND AND SYNTHESIS

W. T. SWANK
USDA Forest Service, 999 Coweeta Lab. Road, Otto, North Carolina 28763

AND

D. A. CROSSLEY, JR.
Department of Entomology, University of Georgia, Athens, Georgia 30602

Abstract. This paper gives a historical sketch, site characteristics, and a general description of the Biosphere Reserve at Coweeta Hydrologic Laboratory, North Carolina. Up-to-date assessment of production values, water chemistry, and physical characteristics of the numerous experimental and control watersheds are provided.

INTRODUCTION

In October 1984, Coweeta celebrated 50 years of long-term hydrologic and ecological research through several events including a three-day symposium. Thirty-five papers covering physical, chemical, and biological process research and watershed-scale experiments with applications to management were presented. This synthesis (Swank and Crossley 1986) will be published in book form and provides an extensive ecosystem data base for a variety of alternative analyses including the development of ground-truth values for high altitude remote sensing systems. In this paper, our objective is to summarize a few components of this extensive data base.

SITE DESCRIPTION

The 2185-ha Coweeta Hydrologic Laboratory is located in the Nantahala Mountain Range of western North Carolina, within the Blue Ridge Physiographic Province (35°N latitude, 83° 30'W longitude). The topography of Coweeta is steep; elevations range from 686 to 1600 m with average side slopes of 50%. The climate of the region is characterized by cool summers, mild winters, and abundant rainfall in all seasons. Average annual precipitation varies from 1700 mm at lower elevations to 2500 mm on the upper slopes. Less than 5% of annual precipitation is comprised of snow. Precipitation has been gauged at over 135 sites during the past 50 years. In general, precipitation increases with elevation at a rate of about 5% per 100 m along the east-west axis of the Coweeta valley but changes little with elevation between opposite facing slopes. Over the past 50 years, 30 climatic stations have been operated at Coweeta. The climatic monitoring network now consists of five fully instrumented stations distributed over the basin. Long-term monthly averages and ranges for several important climatic variables measured in the laboratory administrative area are given in Table 1.

Table 1. Averages and ranges of monthly means for climatic variables at Coweeta CS01

Climatic variable	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Precipitation (mm/month)												
Average	174	181	203	156	140	130	144	139	125	112	139	178
Minimum	50	28	72	13	32	32	9	41	6	1	24	23
Maximum	371	423	433	287	477	318	300	340	333	291	478	388
Evaporation (mm/month)												
Average	34	43	77	97	104	107	108	98	81	67	46	30
Minimum	16	11	50	57	83	79	88	77	60	48	34	14
Maximum	60	76	132	137	133	157	135	120	100	83	57	57
Air temperature (°C/day)												
Average	3.3	4.4	8.0	12.6	16.4	20.0	21.6	21.3	18.4	13.0	7.8	4.1
Minimum	-4.0	-0.4	1.7	10.0	13.4	17.4	19.6	19.5	16.5	10.8	4.8	-0.6
Maximum	10.9	8.8	12.8	15.0	18.8	22.9	23.1	22.8	20.4	16.0	10.9	8.5
Solar radiation (MJ/m^2/day)												
Average	8.0	11.1	14.1	17.8	18.2	19.2	17.9	16.2	14.0	12.5	9.0	7.0
Low	6.0	9.0	10.3	12.9	15.4	14.5	13.9	12.5	12.3	9.2	7.2	5.2
High	10.8	13.6	17.6	21.3	21.4	22.5	24.3	19.8	16.9	17.7	11.1	8.7

There are 69 km of first-, second-, and third-order perennial streams within the basin. The drainage pattern is dendritic, stream channels are generally V-shaped, and drainage density is uniform at 3.15 km•km^{-2}. Permanent weirs were constructed on 32 Coweeta streams, and records were initiated on some streams in 1934. Presently, 16 streams are being continuously gauged. The range of monthly streamflow is rather narrow, but discharge is highest and most variable during February and March and lowest and most stable during late summer and early fall. Large differences in runoff occur between watersheds in the Coweeta Basin in response to differences in rainfall amount, soil depth, evapotranspiration, and topography. The range of physiographic and mean hydrologic characteristics of Coweeta control watersheds are shown in Table 2.

The regolith within the Coweeta Basin is deeply weathered and averages about 7 m in depth. Soils generally occur within two orders--fully developed Ultisols and immature Inceptisols. The underlying bedrock is termed the Coweeta Group and has been mapped and described in detail. The group consists of a series of metasedimentary and possibly metaigneous rocks which overlie the older rocks of the Tallulah Falls Formation of Precambrian origin. This formation is predominantly biotite, muscovite, and garnet. The biotite schist is coarse grained and medium to dark gray, containing biotite, orthoclase, quartz, garnet, and sillimanite. Within the formations are interlayers of pelitic schist, metasandstone to metagraywacke, and minor calc-silicate quartizite.

In 1968, the measurement of annual and seasonal fluxes of select nutrients were initiated for several forested watershed ecosystems in the Coweeta Basin. In subsequent years, the baseline network for precipitation and stream chemistry measurements was expanded and was fully implemented by 1972. Characterization of precipitation and stream chemistry is available for seven control and nine treated watersheds. The chemical composition of bulk precipitation is dominated by H and SO_4 ions (Table 3). Bulk precipitation at Coweeta is characterized as a weak solution of sulfuric and nitric acids that is somewhat buffered by base cations to produce a mean pH of 4.6. Stream water chemistry of low elevation watersheds is dominated by Na, Ca, and Mg cations, while HCO_3 is the dominant anion (Table 3). Thus, stream water is characterized as a cation-bicarbonate solution with a mean pH of 6.7. At high elevations, ionic strength of stream water is reduced by about 50% and SO_4 replaces HCO_3 as the dominant anion.

The long-term mean annual inputs, outputs, and net budgets for control catchments are summarized in Table 4. There is more NO_3, NH_4, and PO_4 added annually in precipitation than is lost in streamflow for all control ecosystems. Net losses occur for Ca, Na, K, Mg, and SiO_2 in all watersheds, a reflection of the dominance of these net budgets by geochemical weathering processes. Chloride is in close balance for most catchments, which supports the reliability of the budget approach at Coweeta to characterize the biogeochemistry of forest ecosystems. The budget for HCO_3 shows a large net loss which reflects the biological production and dissolution of CO_2 within the soil. All controls show large apparent accumulations of sulfate due to soil SO_4 to organic S forms in litter and soil layers.

Table 2. Some physiographic and mean hydrologic characteristics of Coweeta control watersheds

	Characteristic		Watershed					
			2	14	18	34	27	36
(1)	Area	ha	12.26	61.03	12.46	32.70	39.05	48.60
(2)	Maximum elevation	m	1004	992	993	1184	1455	1542
(3)	Minimum elevation	m	709	707	726	852	1061	1021
(4)	Land slope	%	60	49	52	52	55	65
(5)	Record length	yr	37	44	45	18	35	39
(6)	Mean annual precipitation	cm	177.17	187.55	193.90	200.94	245.08	222.25
(7)	Mean annual runoff	cm	85.39	98.81	103.42	117.47	173.74	167.51
(8)	Precipitation - runoff	cm	91.78	88.74	90.48	83.47	71.34	54.74
(9)	Hursh's runoff coefficient = $\frac{(7)}{(6)}$		.482	.527	.536	.585	.709	.754
(10)	Initial flow rate	$1/s/km^2$	24.52	29.46	29.54	36.57	36.30	40.81
(11)	Quickflow before peak	cm	2.22	3.30	2.73	1.83	17.65	11.33
(12)	Quickflow after peak	cm	5.93	6.62	7.00	3.74	34.15	25.86
(13)	Delayed flow	cm	77.20	88.90	93.69	111.91	121.94	130.33
(14)	Storm duration	hr	13.78	13.45	13.50	11.10	29.93	26.75
(15)	Time to peak	hr	4.20	4.65	4.11	3.95	9.31	8.02
(16)	Absolute peak	$1/s/km^2$	68.78	81.12	79.97	75.65	242.60	154.05
(17)	Recession time	hr	9.57	8.81	9.39	7.15	20.62	18.73
(18)	Mean runoff events/year		66	80	79	80	68	68
(19)	Response factor = $\frac{(11)+(12)}{(6)}$		.046	.053	.050	.028	.211	.167
(20)	Hursh's storm runoff ratio = $\frac{(11)+(12)}{(7)}$		.095	.100	.094	.047	.298	.222

Table 3. Volume-weighted mean annual concentrations of dissolved inorganic constituents in bulk precipitation and stream water for Coweeta WS 2[a]

Constituent	Precipitation		Stream water	
	mg/l	µeq/l	mg/l	µeq/l
H^+	0.027	26.64	<0.000	0.2
Ca^{2+}	0.194	9.70	0.583	29.1
Na^+	0.170	7.38	1.22	53.2
NH_4^+	0.095	6.80	.002	0.2
Mg^{2+}	0.041	3.35	0.326	26.9
K^+	0.094	2.41	0.499	12.8
SO_4^{2-}	1.59	33.1	0.450	9.4
NO_3^-	0.143	10.2	.003	0.2
Cl^-	0.271	7.65	0.662	18.7
HCO_3^-	0.074	1.21	4.97	81.5
PO_4^{3-}	0.013	0.42	.006	0.2
Dissolved silica	0.030	--	8.80	--
	Σ+	56.3	Σ+	122.3
	Σ-	52.6	Σ-	109.9

[a] Data span the period 1973-1983 (June-May water year) for all ions except SO_4^{2-} (1974-1983), dissolved silica (1975-1983), and HCO_3^- (1977-1982).

Table 4. Average annual nutrient (kg ha^{-1}) and water (cm) budgets for control watersheds at Coweeta Hydrologic Laboratory

Watershed number	Input	Output	Net difference	Input	Output	Net difference	Input	Output	Net difference	Input	Output	Net difference
	Water			NO_3-N			NH_4-N			PO_4		
2	187	93	+94	2.67	0.02	+2.65	1.78	0.02	+1.76	0.25	0.05	+0.20
14	214	119	+95	3.15	0.05	+3.10	2.14	0.04	+2.10	0.29	0.05	+0.24
18	206	119	+87	2.97	0.04	+2.93	1.97	0.03	+1.94	0.28	0.05	+0.23
27	265	187	+78	4.38	0.34	+4.04	2.54	0.07	+2.47	0.38	0.08	+0.30
32	240	171	+69	3.77	0.04	+3.73	2.52	0.06	+2.46	0.35	0.07	+0.28
34	215	128	+87	3.22	0.04	+3.18	2.24	0.04	+2.20	0.29	0.06	+0.23
36	225	183	+42	3.25	0.14	+3.11	2.15	0.06	+2.09	0.31	0.07	+0.24
	SO_4			Cl			K			Na		
2	29.03	4.10	+24.93	5.07	6.18	-1.11	1.76	4.66	-2.90	3.17	11.43	-8.26
14	33.97	5.67	+28.30	6.98	6.44	+0.54	1.80	4.08	-2.28	4.51	8.73	-4.22
18	32.12	4.90	+27.22	5.72	6.30	-0.58	1.98	4.93	-2.95	3.56	10.31	-6.75
27	39.47	21.14	+18.33	9.44	9.21	+0.23	1.86	4.31	-2.45	5.16	9.07	-3.91
32	40.62	7.74	+32.88	8.35	8.48	-0.13	2.20	5.08	-2.88	5.24	11.18	-5.94
34	34.61	5.46	+29.15	6.60	7.37	-0.77	1.91	4.99	-3.08	4.14	11.58	-7.44
36	35.26	16.57	+18.69	6.21	9.94	-3.73	2.18	5.49	-3.31	3.89	13.79	-9.90
	Ca			Mg			SiO_2			HCO_3		
2	3.63	5.45	-1.82	0.76	3.05	-2.29	0.55	77.25	-76.70	1.27	40.44	-39.16
14	3.83	5.28	-1.45	0.88	3.25	-2.37	0.48	59.09	-58.61	--	--	--
18	4.00	7.03	-3.03	0.85	3.49	-2.64	0.62	83.69	-83.07	--	--	--
27	3.31	6.80	-3.49	1.17	3.87	-2.70	0.46	65.50	-65.04	--	--	--
32	4.25	8.25	-4.00	1.04	4.82	-3.78	--	81.43	--	--	--	--
34	3.90	8.82	-4.92	0.88	4.40	-3.52	0.44	79.81	-79.37	--	--	--
36	4.40	10.80	-6.40	0.93	4.73	-3.80	0.68	106.46	105.78	--	--	--

VEGETATION DESCRIPTION

Vegetation of the Coweeta Basin was traditionally included in the oak-chestnut association, but due to the loss of chestnut to blight, the area is now classified as belonging to the oak-hickory association. Plant communities in the basin are typically diverse for the Southern Appalachians and are distributed over the highly varied topography in relation to temperature and moisture gradients. The composition and structure of the plant communities are still changing in response to past land use history and the loss of chestnut.

A network of about 400 permanent 0.08-ha (0.2-acre) plots distributed over the basin provide the basis for a gradient analysis of vegetation composition (Fig. 1). Four major community types occupy topograpic positions which traverse from mesic coves to slopes to dry ridges and include northern hardwoods, cove hardwoods, oak, and oak-pine. Within the oak type, chestnut oak is the most widespread species and is abundant at middle elevations on slopes with mesic aspects. Scarlet oak is primarily found on drier slopes and ridges. Northern red oak increases in importance at higher elevations (3500 feet) while white oak and black oak are important species at lower elevations. Red maple and hickories are also important components in the oak type.

A variety of watershed experiments, such as cutting and species conversions, have produced a wide range of forest communities with diverse structures. These communities include 30-year-old white pine plantations, even-aged hardwood stands ranging in age from 5 to 40 years, and succession from old field to forest. These communities occupy areas from 6 to 60 ha in size.

BIOMASS, NET PRIMARY PRODUCTION, AND LEAF AREA INDEX

Detailed studies have been conducted on vegetation structure, productivity, nutrient pools, and nutrient fluxes in a variety of forest ecosystems at Coweeta. The standing crop biomass, net primary production, and leaf area index for some of these ecosystems are summarized in Table 5. The aboveground biomass of lower elevation mixed hardwood forests is about 140 t ha^{-1} with an LAI of 6.0, while at high elevations LAI is typically about 3.5; all estimates are for watershed-scale ($\geq$20 ha) populations. These same parameters have been estimated for young successional forests revealing a recovery of net production and LAI following clearcutting. Black locust dominated stands show complete recovery of standing biomass after only 17 years of regrowth, and by age 38 biomass is more than double the uneven-aged hardwood forests. Net primary production of these stands is high and ranges from 11 to 15 t ha^{-1} year^{-1}. At low elevations, leaf-out is usually complete about mid-May, and leaf-fall is largely complete by the end of October. Mountain laurel and rhododendron are the dominant evergreen understory species. They provide an LAI of 0.5 or less in the dormant season, although values can be much higher on some sites occupied by dense stands of these species. There is a phenological gradient in the basin in response to temperature and moisture gradients, with later leaf-out and somewhat earlier leaf-fall at higher elevations.

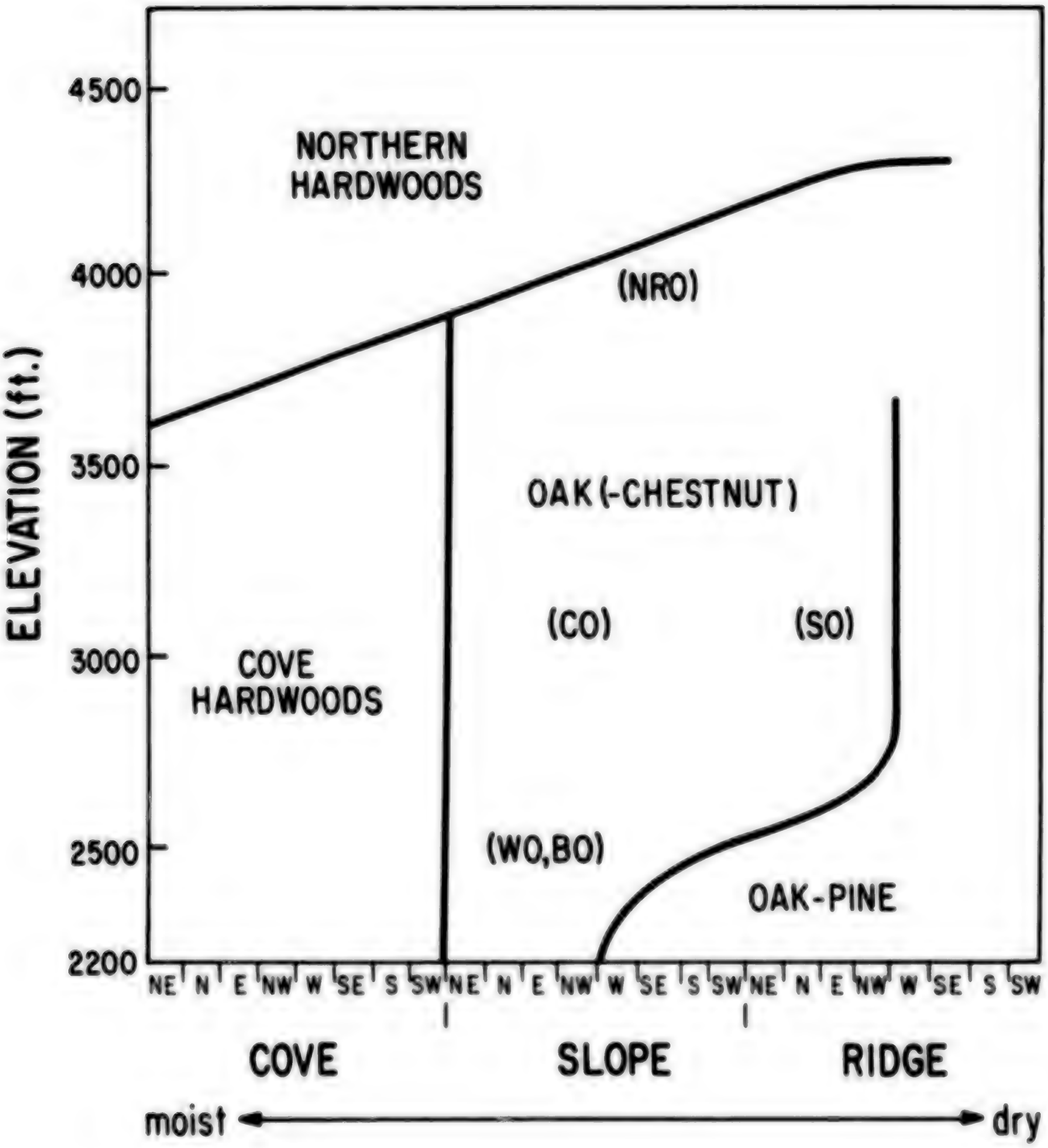


Fig. 1. Major forest types at Coweeta in relation to elevation and aspect. BO = Black Oak, CO = Chestnut Oak, NRO = Northern Red Oak, SO = Scarlet Oak, WO = White Oak.

Table 5. Summary of biomass, net primary production (NPP), and leaf area index (LAI) for selected Coweeta forest ecosystems

Ecosystem	Biomass t ha^{-1}	NPP t ha^{-1} yr^{-1}	LAI m^2 m^{-2}
Oak hickory forest (low elevation)	140.0	8.4	6.0
Oak-hickory forest (high elevation)	--	--	3.5
Even-aged hardwoods (3 years)	9.1	4.2	4.2
Even-aged black locust dominated stands			
4 years	22.	11.5	--
17 years	142.0	14.9	--
38 years	328.0	15.0	--
White pine plantation (15 years)	69.6	13.5	9.9-17.8

The two white pine plantations (now 30 years old) provide a sharp contrast in LAI to hardwood forests. At age 15 the dormant season LAI (all sides of needles) was nearly 10 and increased to 18 in the growing season. Additional estimates of biomass, NPP, and LAI are available from age 10 through age 30 for one of the plantations in addition to the spatial distribution of these parameters over time.

Detailed analyses of nutrient pools and fluxes for most of these ecosystems are also available, and an equally intensive data base is available on stream ecosystem structure and function at Coweeta. Taken together, forest ecosystem characterizations at Coweeta are among the most extensive available and provide an excellent opportunity to develop, test, and modify remote sensing capabilities.

LITERATURE CITED

Swank, W. T., and D. A. Crossley, Jr. (Editors). 1986. Forest Hydrology and Ecology at Coweeta. Springer-Verlag (accepted).

CHAPTER 4. INFORMATION ON THE H. J. ANDREWS EXPERIMENTAL FOREST, WESTERN OREGON CASCADE RANGE

J. F. FRANKLIN
USDA Forest Service, Pacific Northwest Forest and Range
Experiment Station, Corvallis, Oregon

AND

R. H. WARING
College of Forestry, Oregon State University, Corvallis, Oregon

Abstract. This paper reviews the historical development of watershed experiments on the H. J. Andrews Experimental Forest, Oregon, and gives site characteristics and background information on current programs. The site is a Biosphere Reserve and has an active program on Long-Term Ecological Research program funded by NSF. H. J. Andrews represents one of the world's most productive forest ecosystems. and its integrated research base includes the land-water interface.

INTRODUCTION

The H. J. Andrews Experimental Forest (HJA) was established in 1948 by the USDA Forest Service from a part of the Willamette National Forest, Oregon. The primary objective was to provide a site for research and education on old-growth Douglas-fir-western hemlock forests and their conversion to managed stands (see Franklin and Waring 1979).

The HJA consists of the 6000 ha drainage of Lookout Creek and is located in the rugged topography of the Western Cascades approximately 44°N latitude 122°W longitude. Elevations range from 450 to 1650 m. Bedrock consists entirely of volcanic materials--tuffs, breccias, and andesitic flows of Miocene and Pliocene age. The climate is maritime in character with cool, very wet winters and warm, relatively dry summers; very little precipitation occurs during the period of June through September. There are strong orographic influences on precipitation and on the proportion which falls as snow. At higher elevations, winter snowpacks may reach depths of 5 m and persist for 8 months of the year. Because of the mild, wet winters a great deal of the biological activity, such as photosynthesis, goes on during the fall and winter months, even at higher elevations.

Aquatic ecosystems consist almost entirely of streams which range up to fifth order in size (Lookout Creek). Low flows are in late summer and early fall, while maximum flows are associated with winter storms. Ratio of low to high flow is about 1:1000 for the smaller streams.

Forests on the HJA are strongly dominated by conifers, and forest conditions vary markedly along environmental gradients of temperature and moisture. In the low-elevation temperate forest (Western Hemlock) zone characteristic species are: Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), western yew (*Taxus brevifolia*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calcocedrus decurrens*), and bigleaf maple (*Acer macrophyllum*). At higher elevations (above about 1000 m) subalpine forests (Pacific Silver Fir Zone) occur. Characteristic species are Pacific silver fir (*Abies amabilis*), noble fir (*Abies procera*), mountain hemlock (*Tsuga mertensiana*), and western white pine (*Pinus monticola*).

The bulk of the forests at HJA are old-growth stands of about 500-years age, although substantial acreages of young-conifer forests have been created by clearcutting since 1950. Dominance of old-growth forests was a primary reason for the original selection of HJA as an experimental forest. Approximately 80% of the original acreage was in old growth, mostly of 500-year age but with a significant amount of the 275-year-old forest at higher elevations. The other important age class in the primeval landscape was mature forest, which originated following wildfires in the mid-1800s; these forests are generally around 135 years of age today. Approximately 20% of HJA has been clearcut since 1950, resulting in a highly dispersed series of young stands of 10- to 20-ha size.

Both existing and potential natural vegetation (habitat types) have been mapped on the experimental forest. Standing crop biomass values are large, averaging approximately 868 t/ha in the old-growth forests. Leaf area index (LAI) values are among the highest in the world, reaching maximum levels of above 12 $m^{-2} \cdot m^{-2}$ (Franklin and Waring 1979, Marshall and Waring 1986).

PAST, PRESENT, AND PROPOSED RESEARCH

Research at HJA has gone through a series of phases: pre-1950--Corps of Engineers Willamette Basin Snow Laboratory; 1950-1960--timber management research primarily on cutting methods and regeneration; 1960-1970--watershed management research using small watersheds to study effects of logging and roads on water yields, erosion, and nutrient cycling; 1970-1980--ecosystem research as part of the International Biological Program's (IBP) Coniferous Forest Biome, with emphasis on carbon and nutrient cycling; and 1980s--balanced program of basic ecological and ecosystem research and applied forest, wildlife, and watershed management research.

Early Research Program

The early research program at HJA covers the period from 1948 to 1968. During the first decade, the emphasis was on development of the staggered setting approach to clearcutting Douglas fir--development of forest logging and road plans, natural and artificial regeneration, salvage logging, and other similar projects. During the second decade, emphasis was on watershed management and included the first experimental watershed treatments in the region and broad surveys of soil stability problems.

Regeneration and Cutting Methods. HJA was the site for majority of research on effectiveness of staggered setting clearcutting (Timberman 1957). The original concept was to utilize natural regeneration. Research at HJA showed that natural regeneration was not dependable because of (1) infrequent seed crops and (2) severe micro-environmental conditions on many clearcuts. This was one of the major factors in the shift to artificial regeneration, now practiced widely in the Pacific Northwest.

The location of first shelterwood and strip clearcutting in the Region was at HJA (Franklin 1963). This work demonstrated the effectiveness of shelterwoods for regeneration and that well-selected trees would survive exposure and wind. The development of shelterwood cutting in the region also evolved largely from the HJA experiences. The HJA was the location of research on windthrow associated with staggered setting cutting systems (Gratkowski 1956).

Many individual studies were conducted on artificial regeneration (stock size, stock type, season of planting, planting site amelioration, fertilization, and etc.). This was the first location where importance of dry ravel in burying seedlings was recognized.

Watershed Management. Watersheds 1 to 3 were the first experimental watersheds in the region and demonstrated the extreme importance of roads and of mass movements in causing soil erosion. Watershed 1 was completely logged without roads using a skyline crane, while Watershed 3 was 1/3 logged in patch clearcuts using a road system. Erosion losses during the first 5 years were approximately in the ratios of 1:4:100 (control:WS1:WS3). The soil losses in WS#3 occurred as a large pulse soon after treatment with subsequent stabilization while losses in WS#1, while lower, have continued at elevated levels.

Watershed research showed that nutrient losses were generally low following clearcutting in the Douglas-fir region. They did not follow the Hubbard Brook Experimental Forest model of high losses following cutting because, among other factors, nitrification was limited during the summer due to drought and during the winter due to low temperature.

Research throughout the HJA site and surrounding regions showed the extreme slope and road stability problems associated with particular geological formations and soil types (such as hydrothermally altered tuffs and breccias). In effect, a small percentage of the landscape contributes a highly disproportionate part of the mass movements.

General Forest Management. The basic concept of comprehensive forestry logging plans and of parallel (contour) road systems was developed and demonstrated at HJA and Cascade Head (Timberman 1957). The system of salvage logging in mature and old-growth timber using mobile yarder-loader was developed and demonstrated at HJA.

The first west-side habitat type classification was developed in and around HJA and has been used widely in management programs including identification of regeneration problem sites. Two habitat types have been identified as nitrogen deficient sites which should be good candidates for fertilization (Hemlock / Chinkapin and Hemlock / Rhododentron / Salal types).

Each of these phases of research contributed certain facilities, installations, or data bases to HJA. There is a headquarters site with living, office, laboratory, and shop facilities. This is also the location of the central meteorological station which provides continuous records of temperature, wind, precipitation, dewpoint, and radiation. A National Atmospheric Deposition Program sampling site for chemistry of wetfall and dryfall is also maintained at the station. There is also a geographically extensive sampling network throughout the HJA for precipitation, in-forest air and soil temperatures, and stream temperatures.

One of the most important field installations is the series of gauged small watersheds. The first of these sets was installed in the 1950s and was treated in the 1960s. There are three sets of small gauged watersheds:

Watersheds 1, 2, and 3.	Acreage 60 to 100 ha. Watershed 1 was clearcut without roads, Watershed 3 was 1/3 clearcut using roads, and Watershed 2 is the control. Stream flow, temperature, and suspended sediment and bedloads are monitored on all three watersheds, and Watershed 2 is continuously monitored for nutrient content.
Watersheds 6, 7, and 8.	Acreage 10 to 15 ha. Watershed 6 was clearcut, Watershed 7 shelterwood cut, and Watershed 8 is control.
Watersheds 9 and 10.	Acreage approx. 10 ha. Watershed 10 was clearcut in 1975 (part of IBP experiments) and Watershed 9 is control. Continual nutrient as well as hydrologic monitoring is conducted on both.

In addition to these sets of experimental watersheds, the 800-ha drainage of Mack Creek is gauged for continuous records of streamflow and continuously sampled for nutrient content. Stream gauges also exist near the mouth of Lookout Creek and on a comparably size portion of the adjacent Blue River drainage.

A large body of data on forest productivity, biomass and structure, and nutrient budgets has accumulated at HJA as a result of the IBP and subsequent ecosystem research programs. This includes the development of the allometric equations essential for estimation of various ecosystem parameters such as biomass, leaf mass, root mass, leaf area, etc. A variety of specialized studies have also been conducted, including work on root productivity and turnover and detailed tree canopy studies which involved nondestructive sampling of physical, chemical, and biological parameters using climbing techniques.

The forest stands, particularly the old-growth forests, are massive and present significant problems in developing the essential ecological data. Old-growth Douglas-firs are often 100 to 200 cm in diameter and 60 to 80 m in height. Most estimates of biomass and productivity have been done on permanent sample plots (Franklin and Waring 1979) (Table 1). A distinctive feature of these forests is very high levels of biomass ranging to an excess of 100 m^2/ha of basal area and 1000 mt/ha of aboveground biomass. There is also a very high level of necromass, or dead organic matter, in these stands in the form of standing dead trees or snags and of down trees or logs. Typical necromass levels are 150 mt/ha in old-growth forests. A substantial body of information has been developed on this dead woody material or 'coarse woody debris' as it is commonly known.

The permanent plot system at HJA and on associated Research Natural Areas is one of the major research resources. There are several series of such plots. The most extensive set is a series of reference stands which are generally 1-ha permanent sample plots established in mature and old-growth forests representing a wide variety of environmental (and productivity) conditions. There are about 30 of these reference stands with additional, comparable plots at Olympic, Mt. Rainier, and Sequoia National Parks and at the Cascade Head Experimental Forest on the Oregon Coast. Two extensive series of systematically spaced 1/10-ha circular sample plots (Long-Term Ecological Research [LTER] plots) have been established in the old-growth forests of the 100-ha Watershed No. 2 and the mature forests (100-year-old) of the 400-ha North Fork Hagan Creek watershed. In both the reference stands and the LTER plots all trees over 5-cm diameter are monitored, are checked annually for mortality, and are remeasured for growth and recruitment at approximately 5-year intervals.

Two other major sets of permanent sample plots have been established to follow development of early successional vegetation following cuttings of Watersheds Nos. 1 and 3 and No. 10. The Watershed 1 and 3 plots now provide a record of development over 20 years following cutting. The plots on Watershed 10 are now 10 years old. Data are taken on herb and shrub cover and biomass as well as individual trees, once they have attained 1.4 m height. Vegetational changes are occurring very rapidly in these young stands.

Current and Proposed Research

Current research strongly emphasizes the establishment of long-term field experiments with the support of the National Science Foundation's (NSF) LTER program. Experiments installed to date include: a 100-year study of effects of a nitrogen-fixing shrub, *Ceanothus velutinus*, on soil properties and growth of associated Douglas-fir; a 100-year test of the -3/2 thinning law in young Douglas-fir forests with various densities, pruning, and nutritional treatments; and a 200-year study of log decomposition processes in terrestrial and aquatic environments using freshly cut logs placed in a forest or stream system. A major study of the effects of management practices of long-term site productivity is planned for the next 5 years. All of these experiments involve replicated field designs with installations at the scale of at least 10's of meters.

The research group at the HJA makes extensive use of other research sites in the Pacific Northwest and has developed data bases and permanent plots at these other sites. Major efforts are under way at Olympic National Park (includes plots and exclosures in alluvial rain forests); at Cascade Head Experimental Forest near Lincoln City, OR (includes 1/10 to 1 ha permanent plots, some of

Table 1. Data sources for biomass and leaf area in stands in the Pacific Northwest. From Franklin and Waring (1979).

Dominant species	Stand age	Basal area	Aboveground biomass Total	Aboveground biomass Wood[a]	Aboveground biomass Foliage	Projected leaf area	Source and plot identification[b]
Douglas-fir	70	60	422	406	16	8.1	Santantonio (Dry)
Douglas-fir	110	63	661	650	11	5.6	Fujimori et al. 1976
Douglas-fir	100	56	478	466	12	6.1	Franklin (RS 24)
Douglas-fir	120	72	531	509	22	11.2	Santantonio (Wet)
Douglas-fir	125	54	449	437	12	6.1	Gholz 1979 (III)
Douglas-fir	130	90	792	772	20	10.2	Franklin (RS 26)
Douglas-fir	150	72	527	509	18	9.2	Gholz 1979 (IV)
Douglas-fir	150	84	865	849	16	7.4	Gholz 1979 (II)
Douglas-fir	150	90	786	762	24	12.2	Franklin (MR 13)
Douglas-fir	170	72	532	510	22	10.2	Santantonio (Modal)
Group average		71	604	585	19	9.7	
Noble fir	130	98	880	862	18	9.9	Fujimori et al. 1976
Sitka spruce/hemlock	121	100	916	908	8	5.1	Grier 1976 (Plot 12)
Sitka spruce/hemlock	130	118	1,080	1,057	23	14.1	Gholz 1979 (IA)
Sitka spruce/hemlock	140	111	1,492	1,460	22[c]	15[c]	Gholz 1979 (IB)
Group average		110	1,163	1,142	21	13.4	
Western hemlock	26	49	192	171	21	13.4	Fujimori 1971
Douglas-fir/hemlock	250	106	1,117	1,094	23	11.7	Franklin (MR 1)
Douglas-fir/hemlock	250	99	991	968	23	11.7	Franklin (Bagby)
Douglas-fir/hemlock	450	68	715	701	14	7.1	Franklin (RS 1)
Douglas-fir/hemlock	450	84	911	893	18	9.2	Franklin (RS 2)
Douglas-fir/hemlock	450	92	826	801	25	12.7	Franklin (RS 3)
Douglas-fir/hemlock	450	99	1,223	1,203	20	10.2	Franklin (RS 28)
Douglas-fir/hemlock	450	118	1,237	1,208	29	14.7	Franklin (RS 29)
Douglas-fir/hemlock	450	116	1,137	1,107	30	15.2	Franklin (RS 30)
Douglas-fir/hemlock	450	92	1,039	1,018	21	10.7	Franklin (RS 31)
Douglas-fir/hemlock	450	129	1,423	1,392	30	15.2	Franklin (RS 27)
Douglas-fir/hemlock	500	50	317	303	14	7.1	Franklin (MR 6)
Douglas-fir/hemlock	500	81	590	567	23	11.7	Franklin (MR 5)
Douglas-fir/hemlock	500	76	585	559	26	13.2	Franklin (MR 8)
Douglas-fir/hemlock	500	65	606	586	19	9.7	Franklin (MR 4)
Douglas-fir/hemlock	500	89	957	933	24	12.2	Franklin (MR 11)
Douglas-fir/hemlock	750	79	927	908	18	9.2	Franklin (Squaw)
Douglas-fir/hemlock	1,000	69	541	520	21	10.7	Franklin (MR 2)
Douglas-fir/hemlock	1,000	98	789	760	29	14.7	Franklin (MR 3)
Douglas-fir/hemlock	1,000	74	563	539	24	12.2	Franklin (MR 14)
Group Average		89	868	845	23	11.7	

[a] Bole, bark, and branches.

[b] Daniel Santantonio: personal communication; stands located on wet, modal, and dry sites in McKenzie River drainage of Oregon Cascade Range. J. F. Franklin: data on file at Forestry Sciences Laboratory, Corvallis, Oregon. "RS" plots are hectare reference stands or permanent sample plots located at elevations between 360 and 1,200 m on the H. J. Andrews Experimental Ecological Reserve in the Western Cascades of Oregon. "Bagby" is a plot in the Bagby Research Natural Area, Mount Hood National Forest, Oregon. "Squaw" is located in the Squaw Creek drainage, a tributary of the South Fork of the Santiam River, Willamette National Forest, Oregon. "MR" plots are hectare reference stands or permanent sample plots located at elevations below 1,200 m in Mount Rainier National Park, Washington.

[c] Adjusted by R. Waring on basis of additional information.

which were established in the 1930s); Wind River Experimental Forest near Carson, WA (includes permanent plots in mature forests which go back to 1910 and a grid of plots in an old-growth Research Natural Area which goes back to 1948); Mount Rainier National Park; and several areas in the ponderosa pine forests of eastern Oregon.

Current and proposed applied research programs include: (1) specific studies focused on current management problems (e.g., regeneration of the vanillaleaf habitat type) or topics expected to be of major concern in the future (e.g., early commercial thinning) and (2) research based upon application of findings from the basic research programs (e.g., management strategies for riparian zones and for down logs and snags). These are obviously not mutually exclusive; in fact, almost all major basic research projects at the HJA have proved to have management applications, even though the funding source is typically the National Science Foundation.

Regeneration. Major studies are in progress or planned for comparison of silvicultural methods (shelterwood vs clearcutting, various planting treatments, etc.) on the most serious upper-slope and dry-site problem sites. The study of regeneration on the Vanillaleaf habitat type is most advanced and will be followed by similar studies of Xeric (dry, lithosolic) and Beargrass habitat types. The vanillaleaf study will isolate the effects of gophers and competing vegetation.

Long-term effects of snowbrush on Douglas-fir stand development and on soil properties is being established under NSF auspices designed to study effects throughout the rotation. Some short-term research is being carried out on snowbrush X tree interactions. This research should provide a definitive answer to balance between positive and negative effects of snowbrush for at least one major transition zone habitat type. Replication on other habitat types would be highly desirable.

Thinning. A matrix of stands representing different species and stand densities on important habitat types is being established to study effects on stand yields.

Intensive, long-term study of effects of stand density, crown length, and nutrient status on tree growth has been established using NSF funds. This research should provide some very basic information on tree and stand growth response for use in developing stocking level criteria. It also serves to help investigate how individual trees compete differentially for resources.

Research on methods, responses, and problems associated with very early commerical thinnings planned as oldest regeneration stands reach minimal size during the next 5 years. Work of this type is already under way at Cascade Head with a replicated test of commercial thinning in 14" average dbh western hemlock. Treatments were regular thinning to 18- and 24-foot spacings and strip thinning.

Growth and Yield. Several projects have been developed recently. Permanent sample plots for growth and yield studies in young Douglas-fir stands have been established on experimental watersheds.

Permanent sample plots for growth and yield information have been established in several 70- to 130-year-old noble fir stands.

Site index curves for Douglas-fir in dry sites on the Willamette National Forest are currently being developed, using data primarily from stem-dissected trees collected from Blue River south. Site index curves for mountain hemlock are currently being developed using data from Oregon and southern Washington Cascades. Site index curves have been developed for upper-slope Douglas-fir and for noble fir based, in part, on Andrews trees. This research was the first to show the dramatic difference between upper-slope height growth patterns and the McArdle Douglas-fir curves. Upper-slope trees start more slowly but have significant height growth, generally through the second century. A similar pattern exists for trees on hot, dry sites.

Wildlife Habitat. Extensive study is underway of structure and composition of young, mature, and old-growth forest stands with objective or providing quantitative definition of each stage and identification of the major animal species associated with each.

Studies of the ecology of spotted owl have and continue to heavily utilize Andrews as a base site due to large numbers of breeding pairs. Dispersal of fledglings has been wide, but survival has been very poor.

Extensive research has been conducted on the amounts, patterns and rates of decay, and functional roles of snags and logs in forests and streams. Down logs persist much longer than snags of the same size and species; even very large snags will not persist for a rotation, while logs may persist for 200 years or more if not mechanically disturbed. Species, size, and location are all important factors in determining rates of disappearance.

A very long-term study of log decomposition is being established to determine factors affecting rates of decay and log disappearance including size and species. This experiment will provide more controlled conditions than can be obtained by looking at naturally-created down logs. A similar long-term study of types, rates, and factors in snag decay is planned.

General Silvicultural Systems. Long-term site productivity and how it is affected by various management alternatives is planned as major research topic in next 5-year period. The specific plan is to establish long-term study of effects of several residue disposal treatments (including burning vs no burning) on site productivity.

Establishment of areas demonstrating various management alternatives for young stands (e.g., high density/intensive tending vs wider initial spacings) is planned.

Trials of silvicultural approaches for incorporating old-growth and other ecological features (such as snags and down logs) in intensively managed commercial forests are planned.

Watershed and Erosion. Studies are currently under way on factors affecting movement of landslide areas. H. J. Andrews continues to be a benchmark location for full-range erosion research (earthflows, shallow rapid slides, ravel, root throw, etc.) including management impacts and revegetation processes. Data have been incorporated in planning on the Willamette National Forest.

Stream and riparian zones are under intensive study from a variety of viewpoints including fish production, overall biological productivity, streambank stability, and water quality. Riparian areas are proving to be very complex ecosystems. Stable woody debris is an important component of all streams and small rivers in terms of both physical stability and biological productivity. Source areas for woody debris and persistence of woody debris of various sizes, species, and decay states is under way in a variety of stream sizes and forest types. Studies of the dynamics of woody debris in streams are designed to provide criteria for judging stability and planning debris management.

Streamside vegetation provides a rich variety of food sources and ameliorative functions (e.g., cover, temperature control, and erosion reduction). In forested reaches, litter inputs are almost the sole source of energy for the entire stream food chain. The mixture of coniferous trees, deciduous shrubs and trees, and herbaceous riparian growth provides a desirable mixture of energy sources of varying food quality (e.g., red alder (Alnus rubra) and devilsclub are very high) and speed of decomposition (e.g., Douglas-fir needles are slow). As a result of variation in the quantity, quality, and timing of litterfall, a microbially prepared substrate is available for invertebrates and other stream organisms throughout the year.

Research has shown that the ability of a stream to retain material within a reach is very important, partly so food sources can be held until processed and ready for use by stream organisms. Woody debris is one of the most effective ways in which streams retain resources and stability.

Research at HJA and in the Olympics and Coast Ranges is showing that woody debris is also important in larger streams and rivers; removal of materials can result in undesirable loss of aquatic habitat diversity. Logs attached to rootwads anchored in banks are particularly desirable structures in many stream and small river systems.

Streams in clearcuts may be most productive of small fish (provided water quality is maintained) because of better food supply. Streams in young stands are generally least productive, while old-growth streams are intermediate in production but harbor the larger sized fish in pools created from large woody debris.

Integrated Research. One of the major keys to successful research programs at Andrews has been the existence of an integrated research team which includes a variety of disciplines (geomorphologist, plant ecologist, physiologist, soil scientist, entomologist, etc.) involved in a mix of basic and applied research. The most significant research results appear to occur in interdisciplinary areas as a consequence of collaborations in field and data analysis. Many of the most challenging management problems also appear to be interdisciplinary-- for example, cumulative effects, timber and wildlife interactions, and riparian zone management.

LITERATURE CITED

Franklin, J. F. 1963. Natural regeneration of Douglas-fir and associated species using modified clear-cutting systems in the Oregon Cascades. USDA Forest Service Research Paper PNW-3. 14 pp.

Franklin, J. F., and R. H. Waring. 1979. Distinctive features of the Northwestern Coniferous Forest: Development, structure, and function. Pages 59-86 in R. H. Waring (editor) Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings of the 40th Annual Biology Colloquium, Oregon State University Press, Corvallis, Oregon.

Fujimori, Takao. 1971. Primary productivity of a young Tsuga heterophylla stand and some speculations about biomass of forest communities on the Oregon coast. USDA Forest Service Research Paper PNW-123. Pacific Northwest Forest and Range Experiment station, Portland, Oregon.

Fujimori, Takao, Saburo Kawanabe, Hideki Sito, C. C. Grier, and Tsunahide Shidei. 1976. Biomass and primary production in forests of three major vegetation zones of the northwestern United States. Journal Japanese Forestry Society 58:360-373.

Gholz, H. L. 1979. Limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ph.D. thesis, Oregon State University, Corvallis.

Gratkowkski, H. J. 1956. Windthrow around staggered-settings in old-growth Douglas-fir. Forest Science 2(1):60-74.

Grier, C. C. 1976. Biomass, productivity, and nitrogen-phosphorus cycles in hemlock-spruce stands of the central Oregon coast. Pages 71-81 in Western Hemlock Management. University of Washington, College Forest Resources, Institute of Forest Products Contribution No. 34.

Marshall, J. D., and R. H. Waring. 1986. Comparative methods of estimating leaf area in old-growth Douglas-fir. Ecology (in press).

Timberman. 1957. Can there be an orderly harvest of old-growth? The Timberman 58(10):48-52.

CHAPTER 5. HUBBARD BROOK EXPERIMENTAL FOREST BACKGROUND AND SYNTHESIS

R. S. PIERCE
USDA Forest Service, Durham, New Hampshire 03824

AND

T. G. SICCAMA
Yale Forestry School, New Haven, Connecticut 06511

Abstract. This paper outlines characteristics for the Hubbard Brook Experimental Forest in New Hampshire, a designated Biosphere Reserve in the MAB Program. It briefly discusses some of the historical development and summarizes the treatments imparted on the basin. A summary of production on Watershed 6, one that is characteristic of this northern hardwood forest, is provided.

INTRODUCTION

The Hubbard Brook Experimental Forest (HBEF) is a 3160-ha reserve dedicated to the long-term study of forests and streams (Whittaker et al. 1974, Bormann and Likens 1979). Located in the White Mountain National Forest near West Thornton, New Hampshire (Fig. 1), the HBEF was established in 1955 and is maintained by the USDA Forest Service, Northeastern Forest Experiment Station.

BIOSPHERE RESERVE

The HBEF is a Biosphere Reserve (UNESCO's Man in the Biosphere Program) and is the only Biosphere Reserve in the northeastern United States, consequently it is the sole representative of the northern hardwood forest ecosystem.

Beginning in 1963, the Forest Service, Dartmouth college, and later Yale and Cornell universities and the New York Botanical Garden developed the Hubbard Brook Ecosystem Study. Extensive information on the biology, geology, and chemistry of forest and freshwater ecosystems gives understanding for long-term management of natural resources such as water supply, water quality, wildlife, timber yield, and sustained forest growth.

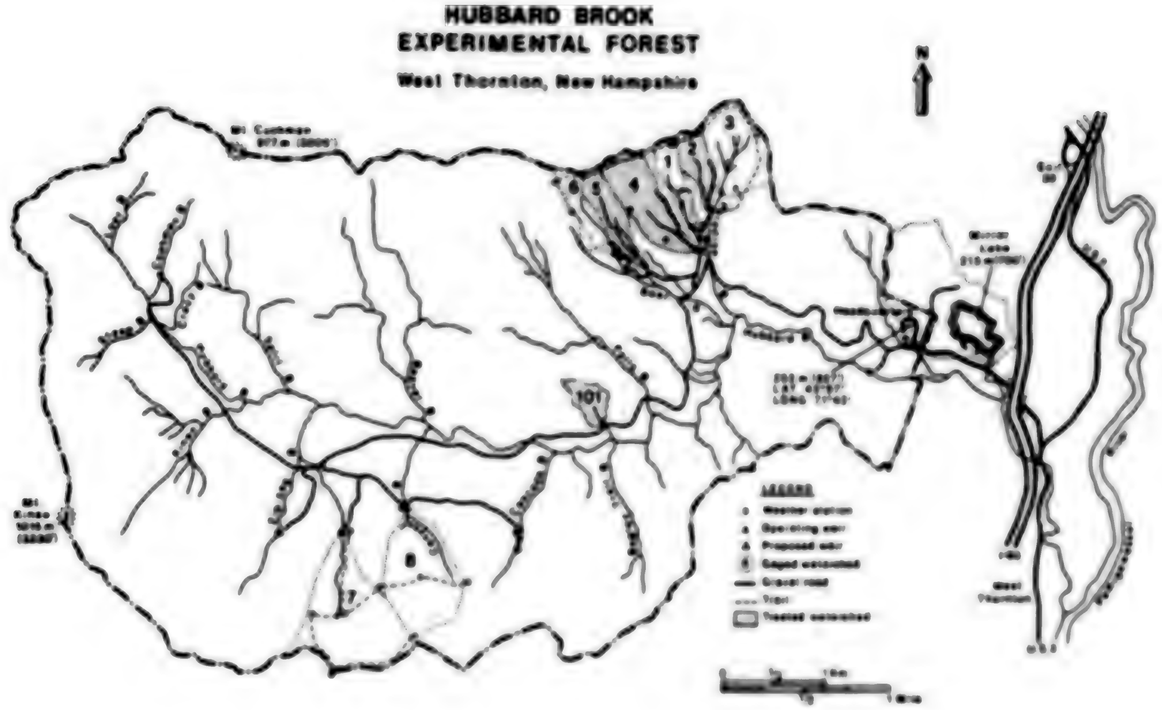


Fig. 1. Location map of Hubbard Brook Experimental Forest, New Hampshire, showing major features, including the principal experimental watersheds.

BEST COPY AVAILABLE

Site Characteristics

The HBEF is located at 43°56' N latitude and 71°45' W longitude. The bowl-shaped drainage basin of the mainstream Hubbard Brook ranges in elevation from 222 m to 1,015 m. The climate is humid-continental with short, cool summers and long, cold winters. The average monthly air temperature is 19°C in July and -9°C in January. The average number of days without killing frost is 100, and the growing season for trees extends from May 15 (approximate time of full leaf development) to October 15 (leaf fall). Average annual precipitation is 140 cm per unit area of forest, with a winter snowpack of about 1.5 m. Average solar insolation is about 11.1 x 10^9 kcal ha^{-1} yr^{-1}. Of the solar radiation received by the Hubbard Brook Valley during the growing season, 15% is reflected, 41% is lost as heat, 42% is used in transpiration and evaporation of water, and 2% supports the biological functions of the entire ecosystem.

Geology and Soils

The bedrock of the Hubbard Brook Valley consists of highly metamorphosed mudstones and sandstones of the Littleton formation, and granitic rocks of the Kinsman formation. An unsorted mixture of boulders, stones, sand, silt, and clay was deposited over the bedrock by glaciers 12,000 to 13,000 years ago (Bormann and Likens 1979). The soil formed by weathering of this glacial till are mostly well-drained, acidic, and of sandy loam texture. The topography is rough with pits and mounds caused by uprooting from falling trees. Soils usually do not freeze during winter because of the thick layer of organic material and the snowpack in winter. The soils are porous, and there is negligible overland flow of water.

A common soil type in the HBEF is the Becket series, a well-drained sandy loam soil with the following general characteristics: an organic layer (4 cm thick) of fresh (Oi) and decomposing (Oe) plant litter at the surface; a 5- to 7-cm thick layer of partly- and well-decomposed organic matter (Oa), pH 3.5; a leached, light gray fine sandy layer about 7 cm thick (E), pH 4.0; the subsoil, extending to a depth of 65 cm, which is dark, reddish-brown fine sandy loam in the zone (upper 15 cm) of organic matter, iron and aluminum accumulation (Bh and Bsl), pH 4.0, brownish-yellow fine sandy loam in the next 23 cm (Bs2), and light olive-brown fine sandy loam in the lower 15 cm (Bs3). Below this to a depth of 100 cm or more is a compact layer of very firm, grayish-brown gravelly loamy sand (C), pH 5.0 (Bormann and Likens 1979).

Water

The HBEF contains numerous headwater streams (Pierce et al. 1970). Stream temperatures range from 0°C to about 18°C. The stream water generally is acidic (pH 4.9) and high in dissolved oxygen but low in the carbon and nutrients which support aquatic life. Flows in the headwater streams range from zero during summer droughts to thousands of cubic meters per hectare each day during storms or snowmelt. Between major storms or snowmelt, these streams carry only small amounts of particulate matter. Most of the 26 kg of sediment annually lost from a hectare of forest are transported during brief periods of high flow.

Mirror Lake is adjacent to the HBEF, and is an integral part of the Ecosystem Study (Likens 1985). It has an area of 15 ha, reaches a maximum depth of 11 m, and discharges into Hubbard Brook. Water entering Mirror Lake comes from precipitation (22%), and surface water and groundwater (78%). Approximately 9% of the water leaving Mirror Lake is evaporated, 48% leaves in the outlet stream, and 43% is lost through deep seepage. This freshwater ecosystem is nutrient-poor; the average pH is 6.0 to 6.4.

Vegetation

Major portions of the HBEF, privately owned at the time, were logged around 1910. Since its acquisition by the USDA Forest Service in 1922, an uneven-aged stand of northern hardwoods, primarily sugar maples (Acer saccharun), American beech (Fagus grandifolia), and yellow birch (Betula alleghaniensis) has developed. On the ridges, rock outcrops, and along the main Hubbard Brook, conifers such as red spruce (Picea rubens), balsam fir (Abies balsamea), and eastern hemlock (Tsuga canadensis) predominate. About 100 species of shrubs and herbs are present. Hobblebush and striped maple form a distinct understory, and Canada mayflower, trout lily, raspberry, and ferns typify the herbaceous groundcover (Bormann et al. 1970).

Populations of algae are limited in the various tributaries of Hubbard Brook. Plants in Mirror Lake range from microscopic phytoplankton to macroscopic water lilies and lobelia (Likens 1985).

Animals

Woodland animals include insects (beetles, springtails, mites, bees, spiders, butterflies); birds (American redstarts, redtailed hawks, ruffed grouse); mammals (snowshoe hares, black bears, white-tailed deer, moose, red foxes, woodland jumping mice, beavers); reptiles (garter snakes, painted turtles); and amphibians (red-backed salamanders, toads). Streams support larvae of the mayfly, stonefly, caddisfly, black fly, midge, and other insects. Mirror Lake includes midges; dragonflies; mosquitoes; invertebrates (rotifers, crustaceans, clams); crayfish; and fish (pike, smallmouth bass, yellow perch).

THE HUBBARD BROOK ECOSYSTEM STUDY

The small-watershed approach to nutrient cycling in ecosystems was pioneered at the HBEF (Whittaker et al. 1974, Bormann and Likens 1979). The technique designates a watershed (catchment) as the basic ecosystem unit for which inputs, outputs, and internal cycling of water, nutrients, and energy can be determined. Small watersheds (ranging from 12 to 76 ha) in the HBEF have well-defined boundaries where the topographic divide coincides with the water divide. Measurements of streamflow on all watersheds over many years suggest that deep seepage is negligible, and that the bedrock is nearly watertight. Thus, precipitation enters the ecosystem and, after short periods of storage in the soil or snowpack, leaves as streamflow or water vapor. For small watersheds at the HBEF, the average annual hydrologic budget is expressed as:

Precipitation (130 cm) = streamflow (81 cm) +
evapotranspiration (49 cm)

Streamflow is 62% of total precipitation, and evapotranspiration is 38%.

The small-watershed approach is used in studies of nutrient cycling because of the close link between the movement of water and nutrients (Likens et al. 1977). Further, precipitation is a major source of sulfur and nitrogen. Weathering of bedrock results in dissolved calcium, potassium, and magnesium. The elements accumulate in living and dead plant material and are cycled within the forest ecosystem. Losses occur as streamflow or gases.

Six adjacent watersheds on a south-facing slope and two adjacent watersheds on a north-facing slope are equipped to measure the amount and chemistry of water. Precipitation collectors are maintained and sampled weekly at 21 locations and elevations. At the bottom of each watershed, a stream flows into a concrete stilling basin and over a V-notch weir. Automatic recorders measure streamflow throughout the year.

The small watersheds at the HBEF have relatively similar geological formations, soils, streams, precipitation, vegetation, and history. These features, along with the long-term records of precipitation and streamflow (>17 simultaneous years for all gauged watersheds), permit extremely close prediction of streamflow. For example, knowing the precipitation and streamflow from one watershed enables streamflow prediction for a nearby watershed to within 5% of actual flow. This capability has permitted intensive studies of the comparative impacts of various treatments on many watershed characteristics.

Long-term records of streamflow on the small watersheds provide a basis for experimental treatments. Selected parameters are monitored in paired watersheds for an appropriate period (perhaps several years), and then one of the watersheds is treated. Results observed from the treatment are compared not only with pretreatment data for the same watershed but also with concurrent records for an untreated watershed. Thus, watersheds are used both to establish baseline information on undisturbed ecosystems and to evaluate the impacts of human-induced disturbances (Whittaker et al. 1974).

Watershed Treatments

Four cutting operations and a variety of related studies have been carried out in the HBEF:

1. Watershed 2 (16 ha). During the winter of 1965-1966 all trees were felled and left on-site. This was followed by three summers of herbicide treatment to prevent vegetation regrowth.

2. Watershed 101 (12 ha). During the autumn and winter of 1970, timber was removed in a commercial, block clearcut.

3. Watershed 4 (36 ha). During the autumns of 1970, 1972, and 1974, progressive strips, 25 m wide, were cut and commercially valuable materials were removed.

4. Watershed 5 (22 ha). During the autumn of 1983 through the summer of 1984, trees larger than 10 cm in diameter at breast height were whole-tree harvested; both the tops and boles were removed.

MAJOR FINDINGS

Fundamental ecological work on a network of reference plots in Watershed 6, a control watershed, has produced background information about HBEF biomass levels. These can be used for general reference in this northern hardwood forest of this age class. In Table 1, standing crop, net change in biomass and annual net production are presented for the period 1965 to 1982. Leaf area index (LAI) averages approximately 6 in northern hardwood forests composed primarily of beech, birch, and maple.

Clearcutting of northern hardwood stands in the HBEF has had dramatic impacts (Table 2).

Recovery of the northern hardwood forest ecosystem during the first decade after clearcutting is marked by the gradual return of water yield and chemistry to precutting levels. Living biomass accumulates over 100 years or more. After an initial decrease, organic matter in the forest floor and dead wood also accumulate. With careful logging and continued use of 70- to 120-year intervals between harvests, clearcutting of northern hardwoods should not have adverse impacts on site nutrient capital, regeneration, or productivity.

HBEF has the longest continuous record (since 1963) of precipitation chemistry in North America, and acid precipitation in the Northeast was first documented here (Bormann and Likens 1979). The average annual pH of precipitation oscillated between 1963 and 1984 but overall, has remained constant at approximately pH 4.1 (unpublished data). Decreasing deposition of sulfate and increasing deposition of nitrate may account for some of this constancy. The origins and complex chemistry of these changes are being investigated. Known effects on forests, streams, and lakes range from beneficial (fertilization resulting from low concentrations of nitrogen, calcium, and potassium) to adverse (toxicity from aluminum and lead).

Composition of the woodland animal community is closely related to quality of the vegetation. For example, the decrease in numbers of least flycatchers, which were found in abundance in 1972-1973 but were seldom seen after 1981, may reflect natural changes in tree species and canopy structure during that interval.

Table 1. Values for all aboveground biomass on Watershed 6 (Siccama, unpublished data)

	Topographic Position				
Years	High	Mid	Low	All	Comments
Hubbard Brook Experimental Forest 1965-1982, and rates of change during those years (Mt/ha) dry wt.					
1965	97.8	144.9	161.6	129.36	> 2 cm dbh
1965	84.5	139.6	155.0	120.5	> 10 cm dbh
1977	155.9	182.2	199.4	175.5	> 10 cm dbh
1982	177.8	184.2	224.6	191.3	> 10 cm dbh
Net change in biomass (> 10 cm dbh)					
1965-1977	71.4	42.6	44.4	55.0	> 10 cm dbh
1977-1982	21.9	2.0	25.2	15.8	> 10 cm dbh
Annual net production (Mt/ha) in > 10 cm class					
1965-1977	5.95	3.55	3.70	4.58	> 10 cm dbh
1977-1982	4.38	0.4	5.04	3.16	> 10 cm dbh

Table 2. Summary of impacts caused by clearcutting on
Hubbard Brook Experimental Forest

- An increase, by as much as 6°C, in temperature at the soil surface.
- An increase in moisture content of the soil.
- Increased concentrations of nutrients, especially nitrate, in the soil solution subject to leaching loss or uptake by plants and microorganisms.
- A maximum increase of approximately 40% in streamflow.
- A 14-fold increase in concentration of nitrate in streamwater, a 3-fold increase in potassium, and a 2-fold increase in calcium after commercial clearcutting.
- No appreciable increase in erosion and sedimentation.
- A decrease by half of the mass of organic matter in the forest floor (over the first 15 years).
- Rapid decomposition and fragmentation of slash (75 to 80% breakdown in the first 14 years).
- Rapid growth of pin cherry and raspberry from seeds which had remained viable in the soil for decades; these pioneer plants conserve nutrients that otherwise might be leached from the site.

The magnitude of these changes was related to the type of disturbance:

- A strip cut (W4) resulted in smaller losses of nutrients by leaching to streams than a block clearcut (W101).
- Large losses of nutrients over several years resulted from clearfelling followed by herbicide treatment to delay regeneration (W2).
- Natural regeneration flourished after commercial harvests; peak densities of pioneer species occurred around 2 years, and a closed canopy was formed by 10 years.
- At year 10, the stripcut (W4) had a more desirable mix of commercial species than the block clearcut (W101), with higher densities of yellow birch and sugar maple and lower densities of pin cherry.

LITERATURE CITED

Bormann, F. H., T. G. Siccama, G. E. Likens, and R. H. Whittaker. 1970. The Hubbard Brook Ecosystem Study: Composition and dynamics of the tree stratum. Ecological Monographs 40:373-388.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Likens, G. E. (Editor). 1985. An Ecosystem Approach to Aquatic Ecology: Mirror Lake and its Environment. Springer-Verlag, New York.

Likens, G. E., F. H. Bormann, R. S. Pierce, J. S. Eaton, and N. M. Johnson. 1977. Biogeochemistry of a Forested Ecosystem. Springer-Verlag, New York.

Pierce, R. S., J. W. Hornbeck, G. E. Likens, and F. H. Bormann. 1970. Effects of elimination of vegetation on stream water quantity and quality. Pages 311-318 in International Symposium on Results of Research on Representative and Experimental Basins. Wellington, New Zealand. International Association of Scientific Hydrology.

Whittaker, R. H., F. H. Bormann, G. E. Likens, and T. G. Siccama. 1974. The Hubbard Brook Ecosystem Study: Forest biomass and production. Ecological Monographs 44:233-254.

CHAPTER 6. REMOTE SENSING AND LANDSCAPE PATTERN IN GREAT SMOKY MOUNTAINS NATIONAL PARK BIOSPHERE RESERVE, NORTH CAROLINA AND TENNESSEE

P. S. WHITE
Cooperative Park Studies Unit, Department of Forestry, Wildlife
and Fisheries, University of Tennessee, Knoxville, TN 37901-1071

AND

M. D. MAC KENZIE
Graduate Program in Ecology, University of Tennessee
Knoxville, TN 37996

Abstract. Remote sensing is a promising tool for the analysis of ecosystem pattern at the landscape level. We are using this technology in one of the most vegetationally complex of all North American landscapes, that of the Great Smoky Mountains National Park Biosphere Reserve. Sources of pattern in this landscape include environmental gradients (controlled by elevation and topography) and disturbances such as settlement history, logging history, fire, the periodic outbreaks of several insect species, and chestnut blight. Multi-spectral scanner data at four scale of resolution (6 m and 15 m aircraft-collected data, 30 m Thematic Mapper data, and 80 m LANDSAT data) are being used to analyze this landscape pattern. We have used remote sensing generated maps to test hypotheses about environmental control of one particular vegetation type (an evergreen shrub dominated community) and plan to build better models of environment using digital terrain data. We have found that optimum resolution varies with characteristics of the object to be interpreted and the purposes of the investigator. We present a simple exercise that predicts optimum resolution from linear dimensions of the objects to be sensed.

INTRODUCTION

A critical problem in contemporary ecology is the analysis of ecosystem pattern at the landscape level. This problem is a challenging one because ecosystems are often patchy in time and space (Pickett and White 1985). Without a quantitative description of landscape pattern, sample selection can be subjective, and sampling design can essentially become arbitrary. In particular, vegetation is chronically undersampled, with sample selection being almost always subjective (e.g., patches of 'mature' vegetation are selected from a heterogeneous matrix). These problems of sampling design are critical because the scale at which ecologists ask questions often falls within narrow bounds (resolution of 10^{-1} to 10^{2} ha: i.e., the scale of stands, watersheds, and landscapes) and because total study area usually exceeds total sample area by three or more orders of magnitude.

Remote sensing represents a promising tool for the analysis of ecosystem-landscape relations. For example, by supplying an appropriate spatial context, remote sensing can improve sample stratification and allow systematic extrapolation from sample points. There are cases in which remote sensing can supplant sampling itself (for example, where it is possible to completely inventory particular ecosystem parameters across large areas using this technology). For the spatial patchiness that results from disturbance, remote sensing can supply a quantitative inventory of patch size and frequency of various ecosystem states. For temporal patterns, repeated imagery can be acquired, leading to quantitative monitoring of ecosystem change. Remote sensing is particularly attractive because these applications are based on quantitative and objective measures (reflectance and emission values). A final advantage is that the data base can be displayed at a variety of scales, can be revised and reproduced easily, and can be manipulated and analyzed, alone and in conjunction with other map data (e.g., digital terrain data).

In Great Smoky Mountains National Park Biosphere Reserve (hereafter, 'GRSM') we have been involved in remote sensing since 1982. The project was recommended in a Man and the Biosphere (MAB) sponsored review of research in the park and was partially funded by the National Park Service MAB coordinator. Our project currently involves multispectral scanner (MSS) data on three scales: 6- and 13-m resolution (aircraft collected) and 30-m resolution (LANDSAT-5, Thematic Mapper). We also have data sets with 80-m resolution (earlier LANDSAT imagery) and plan experimentation with finer resolution (1 to 3 m) in order to assess pre-visual stress in trees related to atmospheric deposition of pollutants. This project is an ongoing one, in which the National Park Service, NASA, and the University of Tennessee have been involved. Although we cannot yet present final results, we will describe our goals (both applied and theoretical), as well as our progress to date. We will describe what we consider to be the full potential of this technology as applied to vegetation science, but the applications we are attempting very much represent a test--there are few published studies based on aircraft-collected data (most of the published material applies to 80-m resolution, LANDSAT data). We know of no other published description of an eastern, montane, site at which aircraft-collected MSS data are being used in vegetation mapping.

Vegetation mapping lies at the center of both our applied and theoretical discussions. However, other ecosystem parameters can be derived from remote sensing, either directly or through extrapolations based on vegetation composition and structure.

SOURCES OF LANDSCAPE PATTERN IN THE STUDY AREA

GRSM is a 208,000-ha preserve in the Unaka Range of the southern Blue Ridge physiographic province (35° 37' N latitude, 84° 30' W longitude). Elevation ranges from 260 to 2,021 m. Climate varies from mesothermal-humid at low elevations to microthermal-perhumid at high elevations (Shanks 1954). At the time of park establishment (1934), 20% of the park was free from major human disturbance (excluding the influence of chestnut blight, which began in the 1920s) and an additional 8% of the park had been disturbed only by diffuse disturbance (Pyle 1985). The rest of the park had been subjected to farming (predominantly at lower elevations) and logging. Since park establishment, several other kinds of disturbances have occurred and constitute major resource management problems. Among the most important have been three exotic species invasions (chestnut blight, balsam woolly aphid, and the wild hog) and atmospheric deposition of pollutants (White and Bratton 1980, Harmon et al. 1983).

The vegetation of the Great Smoky Mountains is a complex mix of evergreen, needle-leaved, and deciduous, broad-leaved forest, with two major types of nonforest vegetation, heath and grassy balds (Fig. 1); Whittaker 1956). The mountains are not high enough for a climatic treeline (Cogbill and White, in press). The highest summits are dominated by red spruce (Picea rubens) and Fraser fir (Abies fraseri). The hardwood/spruce-fir interface represents an important ecotone because it marks the boundary of two contrasting physiognomic vegetation types. This boundary has fluctuated during at least the last 18,000 years in response to changing climate (Delcourt and Delcourt 1984). Southern Appalachian spruce-fir forests are undergoing dramatic change due to an exotic insect infestation and air pollution impacts (White 1984; Cogbill and White, in press). Pronounced successional change is occurring in certain other vegetation types as well. For example, xeric pine stands are succeeding to oak-dominated stands owing to a decreased fire frequency (Harmon 1981) and the periodic outbreaks of the southern pine beetle (Kuykendall 1978). Grassy balds, high elevation grass-dominated areas that were created by clearing and grazing in the early and mid-1800s (Lindsay and Bratton 1979), are being invaded by trees and shrubs.

The two dominant environmental gradients controlling old-growth vegetation distribution in the Great Smoky Mountains are elevation and site moisture class (Fig. 1; Whittaker 1956, Golden 1974). Although these factors explain much of the variance in vegetation distribution, other factors modify the vegetation pattern. As noted above, disturbance forms an overlay to the general environmental control of vegetation (Fig. 1; Harmon et al. 1983, Pyle 1985). There are also subtle and generally unquantified geographic gradients that modify the effect of elevation and site moisture type on the park's vegetation (Harmon 1982, White 1982). The various sources of heterogeneity in the Great Smoky Mountains have produced a landscape that is among the most complex in North America (Whittaker 1956). The general patchiness of the pattern (whether spatial or temporal) is a major reason for our interest in remote sensing applications. Past vegetation studies tend to present an abstract picture of the park's vegetation, with no attention to residual, unexplained, or random pattern and have not supplied aerial estimates of particular vegetation types.

Heterogeneity in the GRSM vegetation pattern consists of patchiness both between vegetation types (some types occur in relatively discrete patches, while others are continuously distributed) and within a particular vegetation type (imposed by patch-wise disturbance and other sources of local heterogeneity). Three aspects of this heterogeneity relate directly to remote sensing applications: (1) the discreteness of the patches (the narrowness of patch boundaries and the contrast between patch and matrix) is important in mapping composition and successional state; (2) internal heterogeneity is important in the spectral constancy of a particular mapping unit (or, indeed, whether a particular vegetation type makes a mappable unit); and (3) the scale that the patchiness

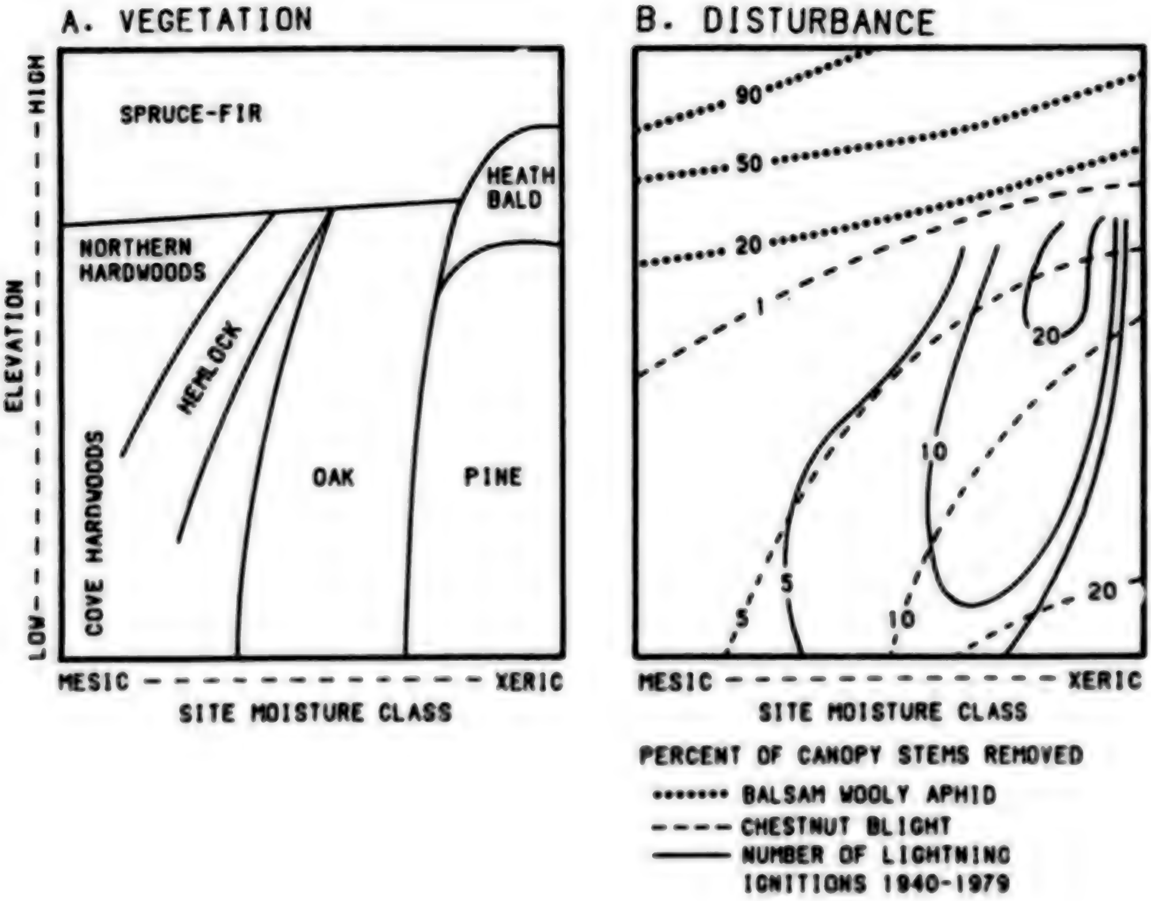


Fig. 1. Vegetation and major canopy altering disturbances in the Great Smoky Mountains (adapted from Whittaker 1956 and Harmon et al. 1983). A. Vegetation. B. Disturbance.

BEST COPY AVAILABLE

occurs on is important in determining the appropriate scale for remote sensing data collection. Coniferous forest types may be especially well suited to remote sensing applications in our study area because they tend to occur in relatively discrete patches in which dominance is concentrated in a few species. Deciduous forests, on the other hand, may show continuous variation within and between types--in this case, the only appropriate model would be one based on individual species populations. One of our major lessons to date has been the determination of appropriate remote sensing scale. We will return to this point below.

An example of pattern and dynamics in the GRSM landscape is supplied by pine-dominated vegetation. This vegetation type is found on dry slope positions (convex topography, upper slope and ridge positions, warm slope aspects) at low to mid elevations. Pine dominance tends to form discrete patches, in part because such stands originated after fire. Periodic outbreaks of the native southern pine beetle kill overstory pines and release understory oaks (Kuykendall 1978), thus hastening succession to deciduous trees. Similarly, fires which are not hot enough to expose mineral soil result in greater importance of deciduous trees in the post-disturbance stand (Harmon 1981). Since fire frequency is lower than in the past, and since park policy continues to be one of suppression, pine dominance is being slowly lost at a rate determined by overstory pine mortality (whether caused by insects, fire, or other factors). The pattern of loss can be determined from remote sensing--we have already been able to identify states of the pine ecosystem using MSS data. Using comparisons with past aerial photographs, we will be able to assess the rate of this loss as well.

However, the problem has more dimensions than those just stated. Beetle kills are rarely complete, thus imposing a degree of patchiness on the pine stands themselves. Further, both fire and beetle outbreaks increase fuel loads in our study area. Those few fires that have been hot enough to regenerate pine in recent times have occurred on such heavy fuel concentrations. Fuel moisture also influences potential fire intensity. Hence, periodic beetle outbreaks, rare droughts, and natural fire potentially interact in the landscape to control pine dominance. Such interactions are likely to produce a heterogeneous and patchy distribution of various successional states of pine forest. The occurrence of severe droughts for several years following years of heavy pine mortality (whether from beetles or fire or both--beetles are drawn to stressed trees) may produce significant pine reproduction. Such events may be infrequent, yet occur on time scales relevant to tree lifespans. In any case, the modeling of this landscape problem, including the short-term goal of assessing pine forest loss, is an example of the potential usefulness of remote sensing in the study area.

GOALS FOR REMOTE SENSING OF ECOSYSTEM PATTERN

Applied Goals

The production of a vegetation map for GRSM is a high priority project because most management activities center on the distribution of the park's plant communities and because these communities are undergoing change. In essence, vegetation mapping is central because the National Park Service mandate ultimately resides at the landscape level. Despite over 200 completed vegetation studies in Great Smoky Mountains National Park (DeYoung et al. 1982), no contemporary all-park vegetation map exists. Human impacts to the elements of this landscape and its overall successional trajectory are also key areas of management concern.

The general objective of vegetation mapping in GRSM is, therefore, to provide managers and researchers with information to better protect resources. More specific objectives are (1) the analysis of major forest change (e.g., air pollution and exotic insect impacts in spruce-fir; possible air pollution impacts in hemlock; succession and fire in pine stands); (2) habitat analysis (e.g., extrapolation of exotic hog impacts; oak mast potential fire fuels levels); (3) automated data base management (e.g., mapping and analyzing park fire history; exotic plant sites; hog removal data; bear relocation data); and (4) miscellaneous (e.g., use of vegetation maps in stratifying and optimizing sample plot location).

Goals Related to the Vegetation Theory

Beyond these applied goals, we also see remote sensing as a way to address fundamental issues in the understanding of vegetation-landscape relations. One of the first objectives in ecological science was the understanding of plant community distribution. At first, this took the form of the description of communities occupying different sites. Subsequently, broadly descriptive models of the distribution of vegetation along single environmental gradients or within multi- dimensional environmental or compositional space (e.g., Whittaker 1967) became dominant. During this evolution there was also a shift from purely qualitative models to explicitly statistical ones (e.g., Loucks 1962). Some statistical models employed direct measures of site environment, while others used synthetic measures (often derived from topography) in order to represent gradients along which many factors changed simultaneously (the 'complex' environmental gradients of Whittaker 1975). Independent of their quantitative sophistication, however, most studies emphasized static views of vegetation and were often based on mature or old-growth vegetation for which the assumption of equilibrium composition as a function of site variables was not blatantly violated.

The emphasis on description of steady state lead to important insights into the organization of communities, but these conceptual gains resulted in an artificial reduction in the dimensions of the landscape-vegetation problem; examination of the processes of disturbance and succession within sites and across landscapes were generally excluded from study design. More recently, research on the role of disturbance has allowed the incorporation of a time dimension, and the importance of disturbance on a variety of spatial and temporal scales has become generally recognized (Pickett and White 1985). However, because this interest is recent and because the problem is inherently complex, quantitative models of ecosystem-landscape relations have been developed only within the last several years (e.g., Paine and Levin 1981, Shugart 1984, Romme and Knight 1982).

Research on the vegetation of GRSM has followed the general development outlined above and has, in fact, provided textbook examples of many enduring paradigms. Whittaker's (1956) mosaic diagrams for the analysis of vegetation pattern in mountainous terrain were developed in the Great Smoky Mountains and have been used widely elsewhere. Whittaker's (1956) demonstration of independent population distribution within continuous coenoclines was, along with the work of J. T. Curtis, an influential model within the developing field of ecology. More recently, the emphasis in the Great Smoky Mountains has shifted from broadly descriptive landscape-vegetation models to more quantitative (e.g., Golden 1974) and processes-oriented studies (Harmon 1984). Within both the Great Smoky Mountains and the field of plant ecology as a whole, the study of disturbance has tended to be carried out within particular community types (Runkle 1981, Barden 1980, White et al. 1985, Harmon et al. 1983); this has the obvious shortcoming that processes studied at one or a series of points cannot be readily extrapolated without additional analysis of temporal and spatial pattern at the landscape level.

An additional limitation of the earlier studies was the reliance on subjective measures of landscape variables. For example, one of the two axes of Whittaker's mosaic chart was site moisture class. This variable was qualitative and subjective and, hence, it is difficult to repeat his studies. Site moisture class was used in an attempt to integrate the combined effects of slope position, aspect, shape, and steepness. These factors, with several others, regulate moisture supply. It is now possible to build quantitative models of environment directly from digital topographic data. These models can be based on hydrologic flow and supply and the relationship between temperature and elevation, precipitation and elevation, and insolation and topography. Hence, we will eventually be able to objectively and quantitatively model the gradients treated subjectively and qualitatively (e.g., Whittaker 1956) or indirectly by other authors (e.g., Golden 1974). Our digital terrain data (on scales of 1:250,000 and 1:24,000) are of sufficient resolution to perform this landscape level-modeling and to test these models at several spatial scales.

The ultimate objective of remote sensing in our view is to test models of population, community, and ecosystem properties from site variables and disturbance. The central null hypothesis for this work is that means and variance in population, community, and ecosystem properties are randomly distributed (and, thus, unpredictable) in the landscape. We state this simple hypothesis for formality; previous research has demonstrated that it will be rejected for most species and ecosystem types. However, remote sensing represents a significant improvement in methodology for addressing landscape questions. It will be possible to completely inventory vegetation, thus avoiding geographic bias, chronic undersampling, and subjective stand selection.

How well will we be able to reach these ambitious goals? We have already determined that 11 evergreen community types in the study area can be accurately censused using our aircraft-collected MSS data. These types are particularly amenable to landscape modeling. Although species populations are independently distributed in the study area, there tends to be a higher rate of vegetation change across deciduous-evergreen boundaries than on either side of this physiognomic transition (White 1976, Siccama 1974). These boundaries may, in part, be sharpened by biological feedback between environment and forest type. Coniferous-dominated stands create effects on internal stand resources in terms of leaf litter quality, decomposition rate, and light seasonality and quality. Where vegetation is not conspicuously patchy, continuous models will have to be employed.

A preliminary trial of our methodology for testing the predictability of vegetation distribution from site and disturbance was carried out using a complete inventory of the 442 heath balds in the park (White et al., in review) and provides justification for the feasibility of our approach. In that trial, heath balds proved to be nonrandomly distributed in the landscape (as determined by testing a random model using elevation, slope aspect, slope position, slope shape, and other variables) and yet occupied fewer than 50% of the sites predicted to be ideal based on topographic variables. Although heath balds had been the subject of a number of descriptive community studies (Cain 1930), the analysis we performed was qualitatively different because we formulated explicit random models. Disturbance was strongly implicated in explaining the difference between predicted and observed heath bald distribution.

DESCRIPTION OF MULTISPECTRAL SCANNER PROJECTS IN GRSM

Past Studies

There have been four earlier attempts to use LANDSAT data in the Smokies. H. R. DeSelm and co-workers analyzed the spruce-fir/deciduous forest interface on 80-m resolution LANDSAT (ERTS) imagery (DeSelm and Taylor 1973, DeSelm et al. 1972). Also in the early 1970s there was an ERTS-based project carried out by NASA in conjunction with the National Park Service to perform "Resource Basic Inventories" for a series of parks, including GRSM. A few reports survive from this project, but it is unclear if the satellite data were used successfully. Between 1976 and 1981, J. S. Olson and M. E. Harmon attempted to interpret vegetation on the Noland Creek, Silars Bald, and Clingmans Dome USGS 7.5' quadrangle maps from LANDSAT data. Forest types, except for broad designations such as evergreen, deciduous, and mixed, were difficult to identify, due both to the inherent resolution in the data and the problem of shadowing within the scene. Ambrosia (1982) described the vegetation associated with very dark features on LANDSAT imagery (again at the 80-m pixel resolution). He concluded much of the dark area was spruce-fir but also had problems with terrain shadows.

Current Studies Using Aircraft-Collected Data

Two flight missions were completed in the park in 1982: March (leaf off) and June (leaf on). Both missions supplied complete photographic coverage (color infra-red) and MSS data sets for the park at approximately 1:38,000. Photographs and data were also obtained at 1:21,000 photographs on several low elevation flight lines designed to provide greater resolution.

The resolution of the MSS data decreases with altitude of the scanner above the terrain at a rate of -2.5 m/100-m altitude. The average picture element (pixel) size of the larger scale data is 13 x 13 m, while the average resolution of the smaller scale data is approximately 6 x 6 m. Since height above terrain on the flight lines varies by approximately 1,600 m, pixel size varies by a total of about 4 m from 11 to 15 m. This variation in pixel size is one of the clear disadvantages of aircraft-collected data.

Taking the average 13 x 13-m pixel size, one complete data set for the park consists of about 12,600,000 pixels, not including overlap between flight lines. For the March flight lines, there were 12 wavelength bands, while the June flight employed a multispectral scanner with 7 wavelength bands. The scanner employed in this latter flight is sometimes referred to as providing 'simulated Thematic Mapper' data, since the bands employed are very similar to those on the LANDSAT-5 (Thematic Mapper). There are no equivalent satellite data to the scanner data from the March flight, although most bands we used in vegetation classification have nearly equivalent bands on both the June and Thematic Mapper data sets. All brightness values represent reflectance except for several true thermal emission channels.

Processing the MSS Data

The raw data were processed using ELAS, a software package developed by NASA. The major analysis steps for each season of data are: (1) basic data editing (statistical procedures to check data values and to correct for reflectance bias across the flight line [ELAS modules RAMP/DRAMP]); (2) classification of pixels using data from four wavelength bands (ELAS module MAXL, a maximum likelihood, unsupervised, classification routine); (3) geographic rectification (rotating the flight lines so data are aligned with true north; referencing the data to a map base with ELAS modules GEOREF and RUBS; this step is necessary in order to use the data with digital terrain data); (4) interpretation and interactive editing of the classified data (includes polygon updating, ELAS module PGUD); (5) data base experiments (use of digital terrain data with MSS data to improve interpretation); (6) merging of flight lines to create a single park data base; (7) field accuracy assessment; and (8) final interpretation, data base editing, and map production. The June flight was found to be the best for vegetation interpretation (on the March flight data, terrain shadows were more marked, and understory evergreen vegetation created reflectance patterns that complicated typing by overstory trees). As described below, we are currently involved with steps 3 and 4 with that data set.

Two problems were initially encountered while working with this data set: a problem with differences in brightness across the flight path, and a problem in geographic rectification. There was a sizable bias in the data created by the geometry of the flight path relative to the sun: one side of the flight line was consistently brighter than the other. The ELAS module RAMP/DRAMP was successfully employed to remove much of this bias.

The second problem was the fitting of the data to a controlled base map. In this case, the ELAS module GEOREF was ineffective; GEOREF had been designed for use with satellite data and could not handle the more complex problems of aircraft data. There are several sources of these problems in aircraft data: (1) slight variation in the flight path; (2) slight wobble of the aircraft around its axis; and (3) the variation in pixel size because height above terrain changes. We found that the error in the GRSM data was about 1%. Across the length of the park, geographic features (mountain summits, stream beds) were displaced by as much as 500 m. Clearly this is not acceptable at any realistic mapping scale (e.g., 1:24,000; 1:125,000).

NASA has recently designed a module for ELAS called RUBS ('rubbersheeting'), which is designed to correct this problem in aircraft-collected data. NASA successfully performed RUBS on one of the GRSM flight lines, reducing errors by more than an order of magnitude to less than 0.1%.

Although the aircraft-collected data have excellent resolution for the park's vegetation, LANDSAT-5 (Thematic Mapper) has several advantages highlighted by the problems just discussed. The satellite platform has greater stability than the aircraft, leading to much less problem in geographic referencing. In addition, much more territory is covered by a single scene (the park occupies about a quarter of a Thematic Mapper scene on each of 2 adjacent paths, vs. the 17 individual March, and 7 individual June aircraft flight lines). This facilitates vegetation interpretation and mapping, since pixel statistics are analyzed and interpreted on a much larger area of the park at one time. Variance in pixel size as a function of terrain is also much less of a problem (the altitude of the satellite is large relative to terrain differences). The satellite passes over the park every nine days on two separate paths. Thus, iterative data sets can be acquired for vegetation interpretation and for monitoring applications. The data are also relatively cheap ($3,600/scene vs. $20,000/aircraft flight). The major problem has been availability: LANDSAT-4 (the original Thematic Mapper) failed soon after launch, and LANDSAT-5 has only been operating for just over one year, prompting delays in particular scenes becoming available.

Vegetation Interpretation

Four raw data channels were used in the vegetation analysis (a green, red, and two infra-red channels), chosen because of their past effectiveness in vegetation interpretations. We used ELAS to perform an unsupervised, maximum likelihood, classification using these four wavelength bands. This classification assigns each pixel a class number (maximum number of classes 64) based on its 4-dimensional resemblance to all other pixels. The class numbers have no meaning in and of themselves; each class is assigned a color (from a 'color table') for visual display. The easiest color table for vegetation interpretation uses the mean reflectance values for each of the four wavelength bands in each class to simulate a color infra-red photograph.

The broad-scale vegetation interpretation is based on reduced and summarized data (the 64 MAXL classes) rather than on the raw data. In addition, the 64 classes are based on only 4 of the available bands. Therefore, there is considerable information in the data set that is not used in the initial interpretation. Work with LANDSAT data showed that conifers in the Northwest were best separated using particular bands and ratios between bands (Walsh 1980). This kind of detailed analysis may become necessary in terms of analysis of deciduous trees.

Reflectance of vegetation varies with solar illumination, sun angle, atmospheric haze, slope angle, slope aspect, slope steepness, water content and temperature of the vegetation, as well as differences among vegetation types and between plant species. Although the mathematics and physics are tractable, if complex, the problem has not been solved directly (i.e., there are no equations based on these factors to predict particular species). Nonetheless, the potential for developments in this area is strong and would increase the ease of interpretation.

In interpreting the MAXL classes, two kinds of problems may occur. First, each vegetation type may be represented by more than one pixel class (e.g., hemlock on a south slope has a different reflectance than hemlock on a north slope). More serious is the second problem: two or more vegetation types may be found within a particular pixel class. The procedure employed here is to edit the data by creating new class numbers. This is the most time-consuming step in the interpretation. When the data are corrected to a controlled map base and can be analyzed using digital terrain data, we will be able to write ELAS processing steps to separate vegetation types.

To date we have found that we can successfully separate the major evergreen vegetation types found in the park, using the 64 MAXL classes alone. We expect to complete the final data base this year. In the high elevation spruce-fir forests, where we have concentrated our initial efforts, we have been successful in separating a series of subtypes (Fraser fir, blown-down fir, standing and fallen aphid-killed fir, spruce-fir, spruce-fir-birch, spruce-birch, spruce-hemlock- birch). In pine stands, we have been able to successfully identify recent beetle-affected areas, regenerating areas after beetle kills, and recent burns (of sufficient intensity to initiate a new stand). Heath balds have been identified easily as well.

Remote Sensing and Scale

The available scales for remote sensing in our study area form a geometric series: pixel sizes are 6 m, 13 m, 30 m, and 80 m. One of our lessons has been that more resolution is not necessarily better--it depends both on the purpose of the investigator and the scale of patchiness in the vegetation that is being analyzed. Too fine a scale of resolution can pick up considerable heterogeneity within the object to be analyzed (e.g., the lit and shaded site of a single tree crown produce different spectral signatures), while too coarse a scale of resolution can average together features that have distinctive properties. These units should be mapped separately (e.g., neighboring stands of coniferous and deciduous vegetation). The goal is to find a scale at which the signature of one pixel integrates the relevant heterogeneity within a unit to be mapped, without causing blurring across boundaries of major cover types.

Key areas of interest in determining optimum scale of resolution include the size of tree crowns, canopy roughness (i.e., smooth canopies will be sensed as more uniform than canopies with irregular shadowing due to the presence of emergent tree crowns), number of species present within the vegetation type to be mapped (species may have very different spectral properties), the shapes and average areal extent of patches of particular forest types, the spectral contrast with the matrix around the forest type, and heterogeneity produced by patchiness within the type (e.g., treefall gaps) (Fig. 2). Since all of these parameters vary between different vegetation types and, within one vegetation type, between different successional states or sites, no one scale of resolution will be perfect for even a single vegetation mapping goal.

The 80-m resolution of early LANDSAT data successfully separated only the most coarse scale vegetation features and tended to average small patches (particularly those with narrow shapes like heath balds and beech gaps surrounded by spruce-fir forest) of vegetation with surrounding types. The aircraft-collected data may have insufficient resolution for addressing pre-visual tree stress where pixel size must be smaller than crown sizes (NASA has proposed a test using sensors at 1- to 6-m pixel scales). Such fine resolution would produce considerable heterogeneity within a forest type and would be inappropriate for vegetation mapping (although it might be ideal for assessing the frequency of small tree fall gaps). Fine-scale resolution not only has the problem of sensing too much detail in terms of individual tree crowns, but the sheer volume of data at that scale would be very costly to preserve and process. The important observation to make is that no one scale will meet all objectives.

If Thematic Mapper data are used in GRSM, the loss in resolution (from 13 x 13-m pixels to 30 x 30-m pixels) will affect the mapping of some vegetation types (e.g., those that are relatively small or narrow, like grassy balds and heath balds), but the data actually may be more appropriate for major forest vegetation types (because the larger pixels are less sensitive to local heterogeneity within the type). We, therefore, plan to test the appropriateness of LANDSAT-5 data to interpretation of the GRSM vegetation.

In order to express the appropriate scale for MSS applications as a function of the dimensions of the objects to be remotely sensed, we carried out a simple exercise. First, we assumed that the objects to be sensed were either circular or linear (with parallel sides), that these objects were internally homogeneous, that the contrast of the objects with their surroundings was absolute, and that their borders were narrow (Fig. 3). We then superimposed a grid of simulated pixels of various sizes on these objects and asked the questions: how many pixels fall within the object, how many on its edge, and how many in the surrounding matrix? The grid was offset from the center of the simulated objects, since there is a low probability that MSS pixels will fortuitously directly overlie a particular object (like a tree crown), but was terminated as soon as most of the grid lay outside the object sensed (Fig. 3). Our results (Table 1) can be used as a guide to predict approximately the maximum pixel dimensions that are compatible with a given sensing problem.

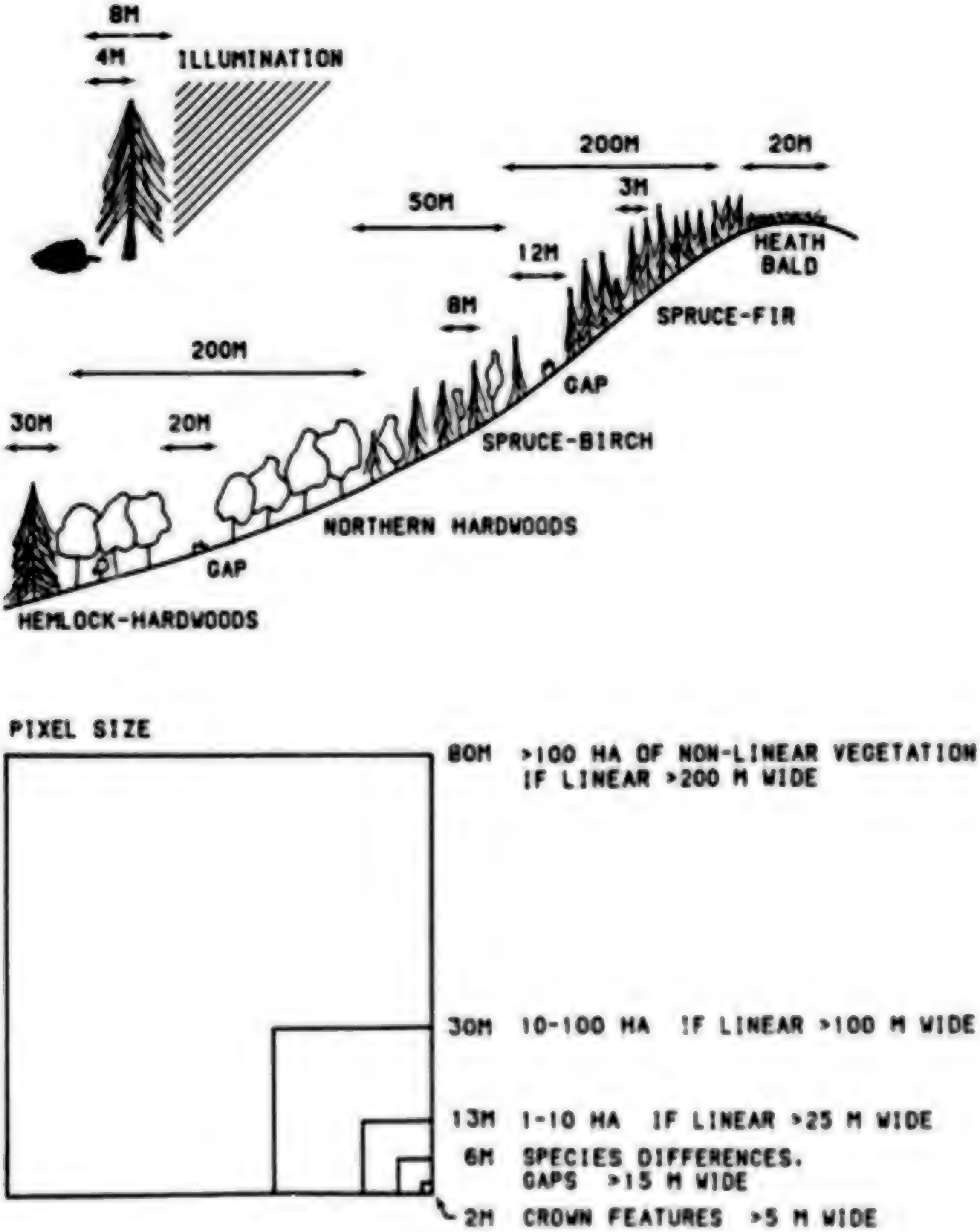


Fig. 2. Picture element (pixel) size and vegetation characteristics.

BEST COPY AVAILABLE

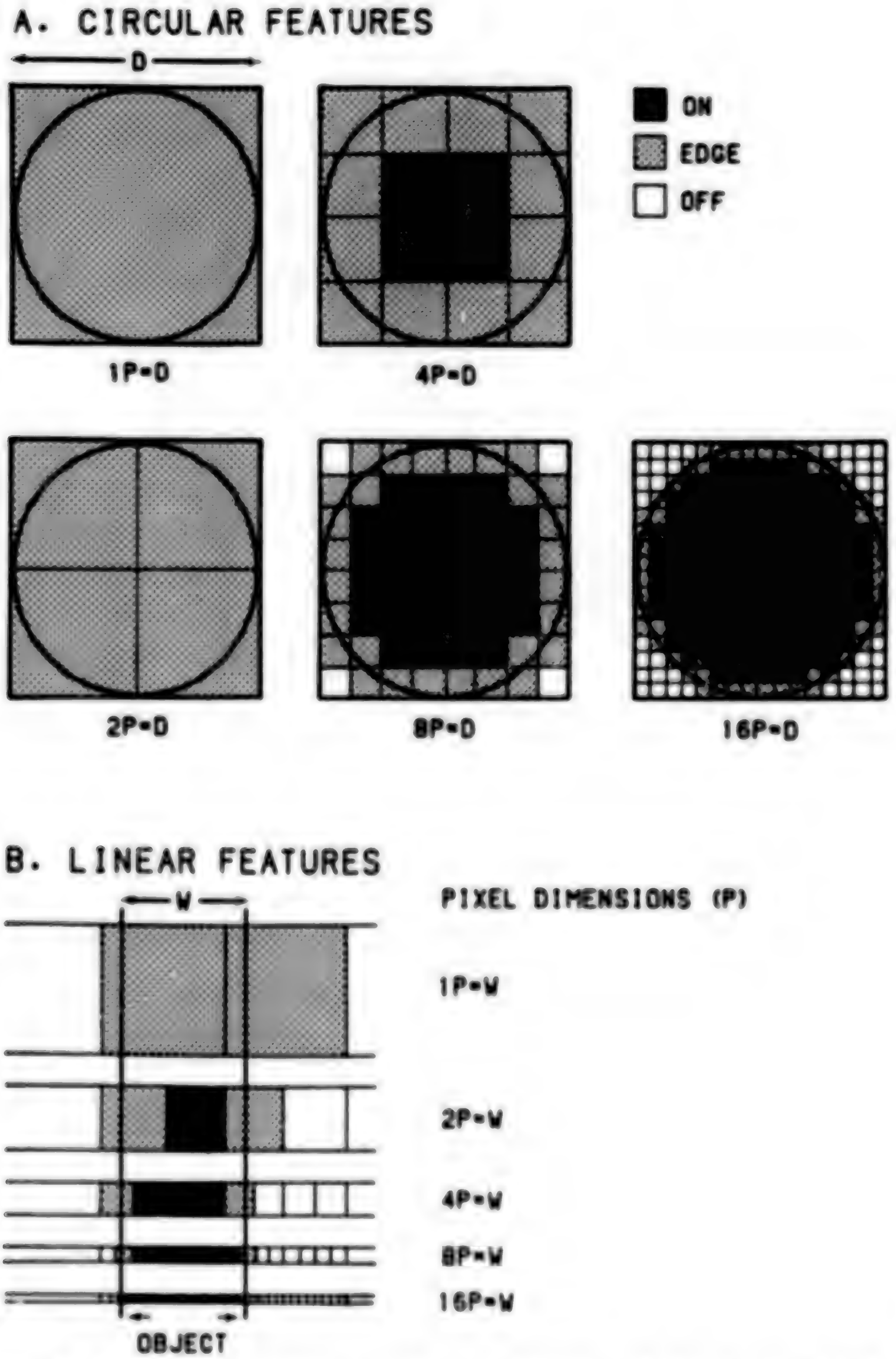


Fig. 3. Determining optimum scale as a function of the diameter (D) and width (W) of objects to be analyzed (p = pixel dimension). A. Circular objects. B. Linear objects.

BEST COPY AVAILABLE

Table 1. An exercise to determine optimum MSS resolution as a function of the dimensions of the object to be analyzed (see text and Fig. 3)

Pixel dimensions:[a]		No. Pixels			% Pixels
Linear	Area	On[b]	Off[c]	Edge[d]	On/(On+Edge)[e]
A. Circular objects					
1	1	0	0	1	0
2	4	0	0	4	0
4	16	4	0	12	25
8	64	32	4	28	53
16	256	164	40	52	76
B. Linear objects					
1		0		2	0
2		1		2	33
4		7		2	60
8		7		2	77
16		15		2	88

[a] Pixel dimensions are based on grid cells that are superimposed on, and completely cover the abstract object to be sensed. The linear dimension is the number of pixels required to equal one width or diameter of the object (1 means that the pixel side is equal to the diameter, 2 means that two pixel sides equal the object diameter and so on). The areal dimension is the number of pixels that are required to completely contain the object and is, thus, the square of the linear dimension. This dimension is irrelevant to the linear object problem in B, where a single row of pixels is used.

[b] The number of pixels 'on' the object is the number directly centered over the object and encompassing no edges.

[c] The number of pixels 'off' the object is the number that fall completely outside the bounds of the object. This is only relevant to circular objects over which a square grid has been imposed, since the grids were terminated as soon as all pixels lay outside the object for linear objects.

[d] The number of edge pixels is the number that fall over and contain object edges.

[e] The ratio of pixels that are 'on' the object relative to pixels that are on the edge of the object, expressed as a percent. The higher the percent, the greater the number of pixels with a relatively pure signature compared to those that average two unlike signatures.

From our work, we postulate that pixel dimensions for circular objects must be at least one-eighth (50% of the pixels occur within the object) and preferably one-sixteenth (64% of the pixels occur within the object) of the diameter of the object. Thus, for tree crowns that average 10 to 30 m in diameter, pixel resolution for within crown sensing of stress should be on the order of 1 to 2 m. For forest types that average 1 ha, the relevant pixel resolution is 6 to 12 m, while for those that average 10 ha, the relevant pixel resolution is 20 to 40 m, and for those that average 100 ha the resolution is 60 to 120 m. For linear features such as heath balds, streams, and roads, the appropriate resolution is one-half the object's width (this would guarantee that at least one pixel would be centered within the object) to one-fourth the object's width (for better resolution). If the object is to map heath balds that are 50 to 100 m in width, then the optimal resolution would be 13 to 50 m. Although these numbers are rough, they suggest the kind of scaling factors that are necessary in the optimal design of remote sensing studies.

CONCLUSIONS

1. Remote sensing supplies a way of objectively measuring landscape pattern and has considerable potential in applied and theoretical studies.

2. The testing of models of landscape pattern will be possible and will be qualitatively superior to past studies because it will be based on the complete inventory of that pattern.

3. Remote sensing can be used to track vegetation change, as in the current break-up of the southern Appalachian spruce-fir ecosystem.

4. The optimal scale of remote sensing will vary with objectives and inherent characteristics of the landscape in question. In many forested montane regions, 80-m pixel data will only be appropriate if the forest types are homogeneous and exist in nonlinear patches of over 100 ha. In GRSM, some vegetation types can be mapped at this scale, but most will only be mappable at 30-m pixel sizes. A few vegetation types in our study area are only mappable at the 13-m pixel scale, while within crown sensing of forest stress will require data at a pixel size of 1 to 2 m.

LITERATURE CITED

Ambrosia, V. 1980. Terrain cover and shadow discrimination from LANDSAT data of the Great Smoky Mountains National Park. M.A. thesis, University of Tennessee, Knoxville.

Barden, L. S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos 35:16-19.

Cain, S. A. 1930. An ecological study of the heath balds of the Great Smoky Mountains. Butler University Botanical Studies 1:177-207.

Cogbill, C. V., and P. S. White. Montane spruce-fir forest and treeline along the Appalachian mountain chain (in press).

Delcourt, H. R., and P. A. Delcourt. 1984. Late-quaternary history of the spruce-fir ecosystem in the southern Appalachian mountain region. Pages 22-35. in P. S. White (editor), The Southern Appalachian Spruce-Fir Ecosystem, Its Biology and Threats. USDI, National Park Service, Southeast Regional Office, Research/Resource Management Report SER-71.

DeSelm, H. R., C. C. Amundsen, and P. F. Krumpe. 1972. Remote sensing of Appalachian wildland resources. Remote Sensing of Earth Resources I:193-205.

DeSelm, H. R., and T. W. Taylor. 1973. Vegetation boundaries on ERTS-1 imagery. Remote Sensing of Earth Resources II:925-933.

DeYoung, H. R., P. S. White, and H. R. DeSelm. 1982. Vegetation of the southern Appalachians: An indexed bibliography, 1805-1982. USDI, National Park Service, Southeast Regional Office, Research/Resource Management Report SER-63.

Golden, M. S. 1974. Forest vegetation and site relationships in the central portion of the Great Smoky Mountains National Park. Ph.D. Dissertation, University of Tennessee, Knoxville.

Harmon, M. E. 1981. Fire history of Great Smoky Mountains National Park--1940-1979. USDI, National Park Service, Southeast Regional Office, Reseach/Resource Management Report SER-46.

Harmon, M. E. 1982. The fire history of the westernmost portion of Great Smoky Mountains National Park. Bulletin Torrey Botanical Club 198:74-79.

Harmon, M. E. 1984. Survival of trees after low intensity surface fires in Great Smoky Mountains National Park. Ecology 65:796-802.

Harmon, M. E., S. P. Bratton, and P. S. White. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. Vegetatio 55:129-139.

Kuykendall, N. W., III. 1978. Composition and structure of replacement forest stands following southern pine beetle infestations as related to selected site variables in the Great Smoky Mountains. M.S. thesis, University of Tennessee, Knoxville.

Lindsay, M. M., and S. P. Bratton. 1979. Grassy balds of the Great Smoky Mountains: Their history and flora in relation to potential management. Environmental Management 3:417-430.

Loucks, O. L. 1962. Ordinating forest communities by means of environmental factors and phytosociological indices. Ecological Monographs 32:137-166.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: Disturbance and dynamics of pattern. Ecological Monographs 51:145-178.

Pickett, S. T. A., and P. S. White (editors). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pyle, C. 1985. Vegetation disturbance history of Great Smoky Mountains National Park-An analysis of archival maps and records. USDI, National Park Service, Southeast Regional Office, Reseach/Resource Management Report (in press).

Romme, W. H., and D. H. Knight. 1982. Landscape diversity: The concept applied to Yellowstone Park. BioScience 32:664-670.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041-1051.

Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecology 35:354-361.

Shugart, H. H. 1984. A theory of forest dynamics. John Wiley, New York.

Siccama, T. G. 1974. Vegetation, soil, and climate on the Green Mountains of Vermont. Ecological Monographs 44:325-349.

Walsh, S. J. 1980. Coniferous trees species mapping using LANDSAT data. Remote Sensing of Environment 9:11-26.

White, P. S. 1976. The upland forest vegetation of the Second College Grant, New Hampshire. Ph.D. Dissertation. Dartmouth College, Hanover, New Hampshire.

White, P. S. 1982. The flora of Great Smoky Mountains National Park: An annotated checklist of the vascular plants and a review of previous floristic work. USDI, National Park Service, Southeast Regional Office, Reseach/Resource Management Report SER-55.

White, P. S. 1984. Southern Appalachian spruce-fir, An introduction. Pages 1-20. in P. S. White, (editor). The Southern Appalachian Spruce-Fir Ecosystem, Its Biology and Threats. USDI, National Park Service, Southeast Regional Office, Res./Resource Manage. Rept. SER-71.

White, P. S., and S. P. Bratton. 1980. After preservation: Philosophical and practical problems of change. Biological Conservation 18:241-155.

White, P. S., M. D. MacKenzie, and R. T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. Canadian Journal Forest Research 15:233-240.

White, P. S., D. A. Stratton, and M. D. MacKenzie. The distribution of heath balds in Great Smoky Mountains National Park (in review).

Whittaker, R. H. 1956. The vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Botanical Review 42:207-264.

Whittaker, R. H. 1975. Communities and ecosystems. MacMillan, New York.

CHAPTER 7. COMPUTER MODELS OF TERRESTRIAL ECOSYSTEMS

H. H. SHUGART
Department of Environmental Sciences, The University of Virginia
Charlottesville, Virginia 22903

and

T. M. SMITH
Department of Environmental Biology, Research School of
Biological Sciences, The Australian National University,
Canberra, A.C.T. 2001

Abstract. This paper reviews needs for models which can express features of forested landscapes that must be considered for new programs attempting to couple remote sensing and ecological subjects. For temperate forest ecosystems three major groups of models are discussed in detail: Markov models, gap models, and spatial forest models. We point out that a major problem in the future will be obtaining information for the validation of these three model families. Work being considered at forested Biosphere Reserves would be invaluable for this validation exercise.

INTRODUCTION

The present discussions of the dynamics of the biosphere and of global ecology come at a time when there is a renewed interest in time and space scales in ecological systems (Olson, Chapter 2; White and MacKenzie, Chapter 6; Pastor and Huston, Chapter 8; and Urban et al., Chapter 10). An appreciation of scales is a clear prerequisite to unifying the dynamics of atmospheric and oceanographic process with the dynamics of the terrestrial surface. Of particular importance is a knowledge of the patterns of dominance (in the sense of controlling pattern) of particular phenomena at particular scales. The categorization of certain phenomena as being important to understanding the space and time scale in a particular ecosystem has been the topic of reviews for several different ecosystems (Delcourt et al. 1983, Pickett and White 1985). In 'hierarchy theory' (Allen and Starr 1982, O'Neill et al. 1986), one sees a focus on expressing relevant mathematical developments in a manner that can provide insight into the ways ecosystems are structured, particularly if they contain complex, multi-level components.

Historically, the complex unraveling of ecological interactions was evident in A. S. Watt's (1925) early work on beech forests and elaborated in his now classic paper on pattern and process in plant communities (Watt 1947). When one inspects Tansley's (1935) original definition of the ecosystem, "These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe to a whole down to the atom. Actually, the systems we isolate mentally are not only included as parts of the larger ones, but they also overlap, interlock and interact with one another," one finds that the same concepts that one sees in hierarchy theory were explicit in the original definition of the ecosystem. Of course, the Watt/Tansely ecosystem paradigm has been introduced as a major ecosystem construct in ecological studies in the United States. One conspicuous introduction of these concepts was Whittaker's (1953) review which used the Watt pattern-and-process paradigm to redefine the 'climax concept' (Clements 1916) that was (and still is) an important construct in American ecology. These same ideas are found in ecosystem concepts developed by Bormann and Likens (1979a&b) in their 'shifting-mosaic steady-state concept of the ecosystem' as well as in what one of us has called a 'quasi-equilibrium landscape' (Shugart 1984).

NONEQUILIBRIUM DYNAMICS OF ECOLOGICAL SYSTEMS

In ecosystems that are dominated by sessile organisms, the temporal dynamics at the scale of the individual organism are almost by necessity nonequilibrium dynamics. This is most apparent in forest systems where the spatial scale of the individual organisms (the canopy trees) is relatively large. The space below a canopy tree has reduced light levels and a considerably altered microclimate due to the influence of the tree. These conditions determine the species of trees that can survive beneath the canopy tree. Upon the death of the canopy tree, the shading is eliminated and the environment is changed. In cases in which the canopy tree dies violently (e.g., broken by strong winds), the changes in the microenvironment are extremely abrupt. The death of the canopy tree initiates a scramble for dominance among the smaller trees that were persisting in the environment created by the canopy tree and seedlings that establish themselves in the high-light environment. Eventually, one of the trees becomes the canopy dominant. The establishment of a new canopy dominant represents the closure of the death/birth/death cycle that can be thought of as the typical small-scale behavior of a forest.

In ecosystems other than forests, but still dominated by sessile organisms, one would expect the same sorts of dynamics. This nonequilibrium behavior at fine spatial scales has been noted in a diverse array of ecosystems including coral reefs (Connell 1978, Huston 1979, Pearson 1981, Colgan 1983); fouling communities (Karlson 1978, Kay 1980); rocky inter-tidal communities (Sousa 1979, Paine and Levin 1981, Taylor and Littler 1982, Dethier 1984); and a wide range of heathlands (Christensen 1985).

The ecosystems that are both historically and currently the most studied in this regard are forests. For this reason it is worthwhile to elaborate the details of the death/birth/death process in forests. In forests, the nonequilibrium dynamics are quasi-periodic with the period corresponding to the potential longevity of the individual organisms. This 'cycle' can be modified by a variety of factors. One important consideration is the manner of death of the dominant tree. Some trees typically die violently or catastrophically and the attendant alterations of environmental conditions at the forest floor (and thus the effect on the regeneration of potential replacements) are very abrupt. Typically these abrupt changes are associated with exogenous disturbances, but there are some species of trees that are 'suicidal' in that mature trees flower but once and die to release canopy space to their progeny (Foster 1977). Some trees tend to 'waste away' before they die so that the changes in the microenvironment that they control are more continuous. Some trees tend to snap at the crown when torn down by winds; others are heaved over at the roots exposing mineral soil. All of these modes of death (and others) influence the stochastic regeneration success of the trees that form the next generation.

It is an open question as to whether mode of death or mode of regeneration is the strongest determinate of pattern of diversity in forests. Both are attributes of the various tree species and may be strongly interrelated. One aspect of the mortality of canopy trees and the associated opening in the forest canopy ('gap formation') in the size of the gap is created. Several authors (van der Pijl 1972, Whitmore 1975, Grubb 1977, and Bazzaz and Pickett 1980) have discussed species attributes that are important in differentiating the gap-size- related regeneration success of various trees. The complexity of the regeneration process in trees and its apparently stochastic nature makes it virtually impossible to hope to predict the success of an individual tree seedling, even if one could determine the attendant environmental factors. Most current reviewers recognize this and tend to discuss regeneration in trees from a pragmatic view that the factors influencing the establishment of seedlings can be usefully grouped in broad classes (Kozlowski 1971a&b, van der Pijl 1972, Grubb 1977, Denslow 1980).

Since the time scales of the replacement cycle in forests are relatively long, tools for better understanding these difficult-to-measure phenomena are individual-tree computer models of forests. These models have been reviewed elsewhere (Munro 1974, Shugart 1984), and the discussion of them here will be brief.

INDIVIDUAL-TREE MODELS OF FORESTS

There are several hundred computer models of forest dynamics based on modeling the responses of individual trees. Reviews of the forestry literature are found in Munro (1974) and a compilation of examples from forestry in Fries (1974). Shugart (1984) reviews several ecological models of forest dynamics and explores the theoretical implications of gap models in particular. The present discussion will treat three different modeling approaches that differ according to the geometric detail in the computation of the interactions among the simulated plants. Markov models simulate the change in state of a simulated area in time; gap models simulate plant-to-plant interactions in the vertical dimension; spatial models simulate the same interactions in two or three spatial dimensions.

Markov Models

Markov models of succession are mathematically and conceptually the most straightforward of the succession models that are presently in use. The models share obvious relationships with other quantitative approaches used in plant ecology. They can be solved by hand (or on a small computer) and are constructed by determining the probability that the vegetation on a relatively small area will be in some predefined condition after a given time interval. It is an essential requirement in formulating these models to have a method of classifying the vegetation into identifiable categories.

The manner in which the vegetation states are classified has varied across applications of Markov models. Horn (1975a&b, 1976) used the species of a canopy tree as the state in a Markov model developed for a forest near the Institute of Advanced Studies in Princeton, New Jersey. The time interval of this particular model was the generation time of canopy trees. Waggoner and Stephens (1971) categorized the forest types according to the most abundant species (in terms of individual trees over 12-cm diameter at breast height - DBH) on 0.01-ha plots located on the Connecticut Agricultural Experiment Station and applied the model over uniform time intervals. These two approaches for identifying the states of the forest [categorization by attributes of a dominant individual as in Horn's (1975a&b, 1976) model] or by attributes of an aggregate of an individuals [as in Waggoner and Stephens (1971) model] represent most of the applications in ecology, although a variety of other classifications could be used. For example, one could categorize a small plot of land by both the species of the largest individual and by the number of individuals (e.g., highly stocked white oak-dominated type, understocked loblolly pine stands, etc.). Hool (1966) used this approach in developing a Markov model of stand change over a large area.

In a Markov model, the number of model parameters is a function of the square of the number of states (or categories in the model). Thus, in the development of a Markov model, one is forced to trade off between the increased resolution in being able to enumerate many different system states and the parameter estimation problems that attend this greater resolution. In Waggoner and Stephen s (1971) simulation, a 40-year-long record of 327 regularly remeasured sample plots was used to compute the model parameters. This means that the change in state of about 16 plots on average was used to estimate each of the transition probabilities. One feature of Markov models is that the relatively uncommon transitions from one state to another need to be estimated with equivalent precision to that of the other more common transitions. This feature creates a need to observe the frequency of occurrence of rare transitions between states and causes an emphasis on large remeasurement data sets as necessary to parameterize a Markov model that has very many states.

An alternative to using direct measurement to determine the parameters of a Markov model is to develop theoretical constructs that allow the estimation of the model parameters on some other basis. For example, Horn (1975a&b, 1976) assumed that the proportion of trees of a given species found growing below a canopy tree indicated the transition probabilities. Noble and Slatyer (1978, 1980) have developed a concept called the 'vital attributes' concept which uses regeneration, response to disturbance, and longevity of plants to determine the parameters of a Markov model. They currently have an 'expert-system' under development on a small 'personal computer'-sized computer, a computer program that queries the user as to the ecological attributes of the species in a successional system and then develops and implements a Markov model of the system. The development of these theoretical methods of estimating the transition probabilities creates the possibility of developing larger Markov models (in which parameter estimation from data normally would be proscribed due to logistic difficulties). The theories used in the parameter estimation should be based on biological attributes of the species. This approach is also found in the more complex models discussed below.

Gap Models

Gap models simulate succession by calculating the year-to-year changes in diameter of each tree on small plots. The plot size is determined by the size of the canopy of a single large individual. Forest succession dynamics are estimated by the average behavior of 50 to 100 of these plots. The growth of each tree is determined by the average competitive influence of the neighboring trees on a plot. Due to the small size of plots, gap formation events (the removal of canopy trees through mortality) strongly affect the resource availability on a plot which in turn affects tree growth (Shugart and West 1981).

The exact location of each tree is not used to compute competition in these models. Tree diameters are used to determine tree height, and then simulated leaf area profiles are computed to devise competition relationships due to shading. These models are spatial in that competition is computed in the vertical dimension. There is an implicit assumption that within a plot of a certain size that the horizontal spatial patterns of the individual plants do not affect the degree of competitive stress acting on an individual to significant degree beyond that accounted for by the plant's height (i.e., tree biomass and leaf area are considered to be homogeneously distributed across the horizontal dimension of the simulated plot).

The regeneration of seedlings on a plot and their subsequent growth is based on the silvicultural characteristics of each species, including site requirements for germination, sprouting potential, shade tolerance, growth potential, longevity, and sensitivity to environmental factors (water and nutrients). Under optimal growth conditions, the growth of a tree is assumed to occur at a rate that will produce an individual of maximum recorded age and diameter. This curvilinear function grows a tree to two-thirds of its maximum diameter at one-half its age under optimal conditions. Modifications reducing this optimal growth are imposed on each tree based on the availability of light and, depending on the specific model, other resources. In most gap models, tree growth slows as the simulated plot biomass approaches some maximum potential biomass observed for stands of the given forest type. Growth is further reduced as climate stochastically varies. Death of individual trees is a stochastic process. The probability of an individual tree's death in a given year is inversely related to individual's growth and the longevity of its species.

Gap model dynamics are based on information concerning the demography and growth of trees during the lifespan of species. The models have a capability to predict the sequence of replacement of species through time and other dynamics on the scale of the average tree generation time. At this scale, the success of a tree at growing into the canopy is more related to the opportunity for inseeding into a plot and the subsequent relative growth rate compared to other seedlings than it is related to the distribution of distances from other competing individuals.

The relationship of the height of the individual to the distribution of heights of competitors is assumed to be sufficient to determine the level of competitive stress experienced by an individual in relation to other trees on the plot. This implies that the distance of a tree to its competitors has no significant influence on the amount of light and other resources available to a given tree. In terms of implementing these models, these assumptions lead to a requirement that the dynamics of a large number of plots be averaged to better estimate the mean rate of success of canopy invasion of each species (Shugart et al. 1981).

Spatial Forest Models

Like gap models, spatial forest models simulate forest dynamics by modeling the establishment, growth, and mortality of individual trees within a defined area. However, spatial models differ from gap models in their explicit consideration of tree position in the horizontal plane. An inherent difference between gap models and spatial forest models is in the form of the competition functions. Because of the explicit consideration of horizontal position, spatial forest models generally use a measure of competition that is a direct function of the proximity and size of neighboring individuals.

Although the competition indices used in spatial models vary greatly in their design, they can be classified into three major categories: (1) distance-based ratios, (2) influence-zone overlap indices, and (3) growing-space polygons.

Distance-weighted size ratios (Hegyi 1974, Daniels 1976) define the degree of competition between a given tree and a neighboring individual as a function of the ratio of the sizes of the two trees (competitor/subject tree) multiplied by the inverse of the distance between the two individuals.

The influence-zone indices (Gerrard 1969, Bella 1971) are based on the assumption of a circular zone of influence around every tree, wherein direct competition occurs (Staebler 1951). The extent to which this area overlaps the influence zone of neighboring trees represents a measure of encroachment and crowding of a tree's optimal functional environment. These indices vary with regard to the type of overlap expressions used (i.e., linear, angular, areal). Growing-space polygons (Brown 1965, Moore et al. 1973, Alard 1974, Pelz 1978, Doyle 1983) represent geometrical designs to calculate nonoverlapping crown area of a tree as limited by the proximity and size of neighboring individuals.

Although each of these indices is based on the relative horizontal position of individuals on the plot, they vary in the methods that are used to determine which neighboring individuals to consider as potential competitors, in defining the size of the zone of influence for a given individual, in consideration of size of competing individuals relative to the target tree, and in their consideration of potential differences in competitive ability among species.

With the exception of Doyle (1983), the above-mentioned competition indices are based on statistical models, and the calculated values of the competition indices are regressed against observed growth rate of individuals to determine the functional relationship between competition and growth. As a result, the functional form of the relationship between the competition index and the growth rate is site specific (related to site factors such as nutrient and moisture availability) and data intensive. For these reasons, most spatial models have been developed for managed forests and, with the exception of the Ek and Monserud (1974) FOREST model, simulate monospecific stands.

CONCLUDING REMARKS

There presently exists a wide array of ecological models of forested landscapes that could be used with considerable advantage in projecting the long-term consequences of small-scale changes in terrestrial processes. The testing of such models is, at this point in time, a considerable challenge, and the data sets that can be used to test such models are in general hard to develop (see Shugart 1984 for general discussion of model validation especially with regard to gap models), but data such as are being developed at some of the Biosphere Reserves represent information that could be used for model tests. Other applications at these sites include the prediction of the expected response of the landscape to various types of disturbances, determination of critical sizes of the landscape units that are needed to average away the effects of natural disturbances, and the determination of the expected range of temporal variation in a landscape unit. The challenge in incorporating landscape-inventory with ecological models is to some degree related to the differences in the time and scale scales in the most efficient techniques for monitoring (remote-sensing) and the time and scale scales in the models. Models of the future will require even more sophistication than developed to date, particularly for expressing the interactions in temporal and spatial scales. For this work we urge new approaches, much like has happened during the developmental history of microscopy in biology. An ultimate goal for modeling studies might well be the development of a "telescoping" model which is capable of being focused on several scales, much like a modern zoom microscope provides for biologists today.

ACKNOWLEDGMENTS

Research supported by the National Science Foundation's Ecosystem Studies Program (Grant Number BSR-85-10099) to the University of Virginia.

REFERENCES

Alard, P. G. 1974. Development of an empirical competition model for individual trees within a stand. Pages 22-37, in J. Fries (editor), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, Sweden.

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: Perspectives for Ecological Complexity. University of Chicago, Press, Chicago.

Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession. Annual Review of Ecological Systems 11:287-310.

Bella, I. E. 1971. A new competition model for individual trees. Forest Science 17:364-372.

Bormann, F. H., and G. E. Likens. 1979a. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Bormann, F. H., and G. E. Likens. 1979b. Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist 67:660-669.

Brown, G. S. 1965. Point density in stems per acre. Forest Research Institute. New Zealand Forest Service, Forest Research Notes No. 38.

Christensen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 86-100, in S. T. A. Pickett and P. S. White (editors), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Institute Publication 242. Washington, D.C.

Colgan, M. W. 1983. Succession and recovery of a coral reef after predation by Acanthaster planci (L.). Proceedings of the International Coral Reef Symposium, 4th. Manilla, 1981 2:333-338.

Connell, J. H. 1978. Diversity in rain forests and coral reefs. Science 199:1302-1310.

Daniels, R. F. 1976. Simple competition indices and their correlation with annual loblolly pine growth. Forest Science 22:454-456.

Delcourt, H. R., P. A. Delcourt, and T. Webb. 1983. Dynamic plant ecology: The spectrum of vegetational change in space and time. Quaternary Science Review 1:153-175.

Denslow, J. S. 1980. Gap partitioning among tropical rain forest trees. Biotropica 12 (Suppl.):47-55.

Dethier, M. N. 1984. Disturbance and recovery in intertidal pools: Maintenance of mosaic pattern. Ecological Monographs 54:99-118.

Doyle T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. Pages 56-73 in D. C. West, H. H. Shugart, and D. B. Botkin (editors), Forest Succession: Concepts and Application. New York, Springer-Verlag.

Ek, A. R., and R. A. Monserud. 1974. FOREST: Computer model for the growth and reproduction simulation for mixed species forest stands. Research Report A2635. College of Agricultural and Life Sciences, University of Wisconsin, Madison.

Foster, R. B. 1977. *Tachigalia* *versicolor* is a suicidal neotropical tree. Science 268:624-626.

Fries, J. (editor). 1974. Growth Models for Tree and Stand Similation. Department of Forest Yield Research, Royal College of Forestry, Stockholm Research Notes 30.

Gerrard, D. J. 1969. Competition quotient: A new measure of the competition affecting individual forest trees. Michigan State University Agricultural Experiment Station Research Bulletin No. 20.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Review 52:107-145.

Hegyi, F. 1974. A simulation model for managing jack-pine stands. Pages 74-90, *in* J. Fries (ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, Sweden.

Hool, J. N. 1966. A dynamic programming-Markov chain approach to forest production control. Forest Science Monographs 12:1-26.

Horn, H. S. 1975a. Forest Succession. Scientific American 232:90-98.

Horn, H. S. 1975. Markovian properties of forest succession. Pages 196-211, *in* M. L. Cody and J. M. Diamond (editors), Ecology and Evolution in Communities. Harvard University Press, Cambridge.

Horn, H. S. 1976. Succession. Pages 197-204, *in* R. M. May (editor), Theoretical Ecology. Blackwell Scientific Publications, Oxford.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81-101.

Karlson, R. H. 1978. Predation and space utilization patterns in a periodically disturbed habitat. Bulletin of Marine Science 30:894-900.

Kay, A. M. 1980. The organization of sessile guilds on pier pilings. Ph.D. Thesis. University of Adelaide, South Australia.

Kozlowski, T. T. 1971a. Growth and Development of Trees: Vol. I. Seed Germination, Ontogeny and Shoot Growth. Academic Press, New York.

Kozlowski, T. T. 1971b. Growth and Development of Trees: Vol. II. Cambial Growth, Root Growth and Reproductive Growth. Academic Press, New York.

Moore, J. A., C. A. Budelsky, and R. C. Schlesinger. 1973. A new index representing individual tree competitive status. Canadian Journal of Forest Research 3:495-500.

Munro, D. D. 1974. Forest growth models, A prognosis. Pages 7-21, in J. Fries (editor), Growth Models for Tree and Stand Similation. Department of Forest Yield Research, Royal College of Forestry, Stockholm Research Notes 30.

Noble, I. R., and R. O. Slatyer. 1978. The effect of disturbances on plant succession. Proceedings Ecological Society Australia 10:135-145.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. A hierarchical concept of the ecosystem. Princeton University Press, Princeton, New Jersey (in press).

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. Ecological Monographs 51:145-178.

Pearson, R. G. 1981. Recovery and recolonization of coral reefs. Marine Ecology: Prog. Ser. 4:105-122.

Pelz, D. R. 1978. Estimating tree growth with tree polygons. Pages 172-178, in J. Fries, H. E. Burkhart, and T. A. Max (editors), Growth Models for Forecasting of Timber Yields. School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University FWS-1-78.

Pickett, S. T. A., and P. S. White (Editors). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Shugart, H. H. 1984. A Theory of Forest Dynamics. Springer-Verlag, New York. 278 pp.

Shugart, H. H., and D. C. West. 1981. Long-term Dynamics of Forest Ecosystems. American Scientist 69:647-652.

Shugart, H. H., D. C. West, and W. R. Emanuel. 1981. Patterns and dynamics of forests: An application of simulation models. Pages 74-79, in D. C. West, H. H. Shugart, and D. B. Botkin (editors), Forest Succession: Concepts and Applications. Springer-Verlag, New York.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. Ecology 60:1225-1239.

Staebler, G. R. 1951. Growth and spacing in an even-aged stand of Douglas-fir. M. F. Thesis, University of Michigan.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.

Taylor, P. R., and M. M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. Ecology 63:135-146.

van der Pijl, L. 1972. Principles of Dispersal in Higher Plants. Springer-Verlag, Berlin.

Waggoner, P. E., and G. R. Stephens. 1971. Transition probabilities for a forest. Nature 225:93-114.

Watt, A. S. 1925. On the ecology of British beechwoods with special reference to their regeneration. Part 2, Sections II and III. The development of the beech communities on the Sussex Downs. Journal of Ecology 13:27-73.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Whitmore, T. C. 1975. Tropical rain forests of the Far East. Clarendon Press, Oxford.

Whittaker, R. H. 1953. A consideration of climax theory: The climax as a population and a pattern. Ecological Monographs 23:41-78.

CHAPTER 8. PREDICTING ECOSYSTEM PROPERTIES FROM PHYSICAL DATA: A CASE STUDY OF NESTED SOIL MOISTURE-CLIMATIC GRADIENTS ALONG THE APPALACHIAN CHAIN

JOHN PASTOR
Natural Resources Research Institute, Duluth, Minnesota 55811

AND

MICHAEL HUSTON
Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831

Abstract. A forest stand simulation model is described that predicts ecosystem properties such as biomass, leaf area, soil carbon, and available nitrogen, using climate and soil data that can be obtained from remote sensing or other sources. Simulation results demonstrate the effect of soil variability within climatic zones on forest species composition, successional patterns, and ecosystem properties. Model predictions compare favorably with data from New Hampshire (Hubbard Brook) and North Carolina (Coweeta). They suggest that soil differences in field capacity have a larger effect on vegetation and ecosystem properties at Hubbard Brook where the annual precipitation is lower than at Coweeta.

INTRODUCTION

The ultimate goal of biological remote sensing is to monitor and predict spatial and temporal variation of biomass and productivity, upon which all life on earth depends. While direct measurement of greenness has shown the value of remote sensing in arid regions (Tucker et al. 1985), problems with multilayered canopies and the required ground-truth data may limit the applicability of this direct approach.

An alternative approach is to combine direct measurements with models that estimate biomass and primary production from physical parameters (climate, soils) obtainable from remote sensing as well as other sources, and which have been or can be validated in the field. Models based on general ecological principals not only can provide estimates based on current physical conditions, but can also make projections about future trends. They can help sort out the effects that several covarying factors have on ecosystem properties, such as climatic, topographic, and soil properties all of which determine water availability. Potential applications include predicting the effects of CO_2-induced climatic change on net primary production. To the extent that future developments in remote sensing technology will allow measurement of soil water availability and canopy chemical composition, models will be needed to integrate these data to estimate ecosystem properties.

Variability within units resolved by remote sensing techniques may be critical for estimating landscape scale properties. For example, variation in soil water availability within climatic zones can cause large variation in ecosystem properties (Monk 1966, Van Cleve et al. 1983, Pastor et al. 1984, Pastor and Post 1986), and thus introduces uncertainty in regional averages obtained from remote sensing. Models can be the critical link between regional remote sensing and validation at a few intensively studied sites. As an example of this approach, we will discuss how a particular model can be used to assess the influence of soil moisture gradients nested within climatic gradients on ecosystem properties.

THE JABOWA/FORET CLASS OF FOREST MODELS: BRIDGES BETWEEN SITE AND REGIONAL STUDIES

The JABOWA/FORET class of forest ecosystem models (Botkin et al. 1972, Shugart and West 1977, Shugart 1984) is eminently suited to the task of integrating site-specific and ecosystem subjects because it can predict ecosystem properties resulting from interactions between individual trees and resources affecting their growth, and because species to which these trees belong are characterized by their continent-wide behavior with respect to climate and soil water availability. A major impetus in the development of these models was to find a way to codify the wealth of information, often anecdotal, obtained from earlier ecological and forestry studies (Botkin 1981). Therefore, these models also serve the role of a bridge between classical Gleasonian ecology and more recent ecosystem studies (Pastor and Post 1986).

When first developing this modeling approach, only species responses to temperature and light were considered (Botkin et al. 1972), and separate models were developed for different sites (Shugart 1984). Solomon et al. (1984) generalized the FORET model for 72 upland species of eastern North America, resulting in a model which can examine changes in ecosystem properties along climatic gradients. Mann and Post (1980) provided a means of predicting species responses to soil water availability, thus enabling the use of these models to examine variability within a climatic zone due to soil moisture gradients. Aber et al (1982) greatly improved the JABOWA model by providing a means of assimilating data on nutrient dynamics during organic matter decay and differential species responses to soil nutrient availability. Pastor and Post (1985, 1986) combined the approaches of Mann and Post (1980), Aber et al. (1982) and Solomon et al. (1984) and incorporated more recent data on soil processes, yielding a model, called LINKAGES, which predicts changes in ecosystem properties and species composition as functions of the interaction between soil nitrogen and water availabilities, climate, and light.

The assumptions of LINKAGES are:

1. the chemical quality of a species litter, actual evapotranspiration, and canopy openings determine decay rates and soil nitrogen availability (Meentemeyer 1978, Aber et al. 1982, Melillo et al. 1982, Pastor and Post 1985, 1986);

2. light availability is a negative exponential function of leaf area or biomass (Botkin et al. 1972, Monsi et al. 1973);

3. the northern and southern edges of a species range indicate the minimum and maximum degree days tolerated (Botkin et al. 1972);

4. species are shade tolerant or intolerant (Botkin et al. 1972, Shugart and West 1977);

5. in eastern North America, the western edge of a species range and the effect of drought on tree growth is determined by how long soil water storage is below wilting point (Basset 1964, Mann and Post 1980);

6. a species can have one of three responses to nutrient availability (Mitchell and Chandler 1939, Aber et al. 1982);

7. the growth of an individual tree is limited by light, nitrogen, water, or temperature, whichever is most restricting; and.

8. the reproductive potential of a species is restricted by the joint effects of temperature, light, and water (Bourdeau 1958).

From these assumptions, LINKAGES predicts species composition, biomass, net primary productivity, soil carbon content, and nitrogen availability across soil moisture gradients for a wide variety of northern temperate forests (Pastor and Post 1986). Pastor and Post (1986) conclude that much variation in ecosystem properties within a climatic zone can be attributed to species replacement along gradients of soil water availability, with differences in species litter causing changes in nitrogen availability, which in turn largely determines net primary productivity.

A CASE STUDY OF NESTED SOIL WATER-CLIMATIC GRADIENTS

What does this model predict regarding the relative importance of soil water gradients nested within broader climatic gradients? The problem is particularly acute in mountain chains because the irregular topography forms short soil moisture gradients within longer climatic gradients up the mountains or along the chain. The Appalachian Mountains demonstrate particularly well the effects of nested gradients on species distribution and ecosystem functioning (Whittaker 1956, 1966). Running in a northeasterly-southwesterly direction for 2500 km, they span warm temperate, cool temperate, and boreal life zones along their main axis and along the elevation of several major peaks. Bands of vegetation along climatic gradients are strikingly evident on any vegetation map or satellite photograph of eastern North America. Variations in soil texture and depth, slope, and aspect cause steep gradients in soil water availability, resulting in major changes in ecosystem properties within climatic regions. (Whittaker 1966, Whittaker et al. 1979).

Model runs were organized according to a split-plot design, soils of two contrasting water holding capacities nested within two climates. Climates simulated were for the South Climatic Division of New Hampshire and the Southern Mountains Climatic Division of North Carolina (U.S. Dept. of Commerce 1968, 1982). The Hubbard Brook and Coweeta Experimental Forests are within these climatic divisions, respectively. Climates of these forests are somewhat cooler and moister than for the regional norms (Table 1). The soils simulated were a 60-cm thick silt loam (field moisture capacity 20 cm, wilting point 10 cm) and a 60-cm thick sandy loam (field moisture capacity 11.2 cm, wilting point 5.0 cm). These characteristics span the range of the more common soils of northern and southern portions of the Appalachian chain (Johnson and Swank 1973, Likens et al. 1977). Initial forest floor humus weight was 65 Mg/ha and N content was 1.30 Mg/ha.

Twenty model runs for two hundred years were made for each soil-climate combination. Mean monthly temperature and precipitation, probability of recruitment and mortality, and initial size of each new sapling varied stochastically. Means of the 20 runs are reported. Each run was begun with no vegetation present. No restriction was placed on species recruitment which might conform to historical patterns of cutting or grazing in these areas (Johnson and Swank 1973, Bormann and Likens 1979).

The simulations indicate that differences in climate cause more variation in ecosystem properties than differences in soil moisture, and that the effect of soil moisture varied with climate, ecosystem properties, and time in succession (Figs 1 and 2). Simulated leaf area, nitrogen availability, net primary production, and biomass were all greater under North Carolina climate than New Hampshire, regardless of soil type. This is consistent with documented differences between the two sites. Soil water capacity caused a greater variation in these properties in New Hampshire than in North Carolina, possibly because of the lower precipitation inputs in New Hampshire (Table 1). In both climates, leaf area, biomass, and net primary production were more affected by soil water capacity than was nitrogen availability.

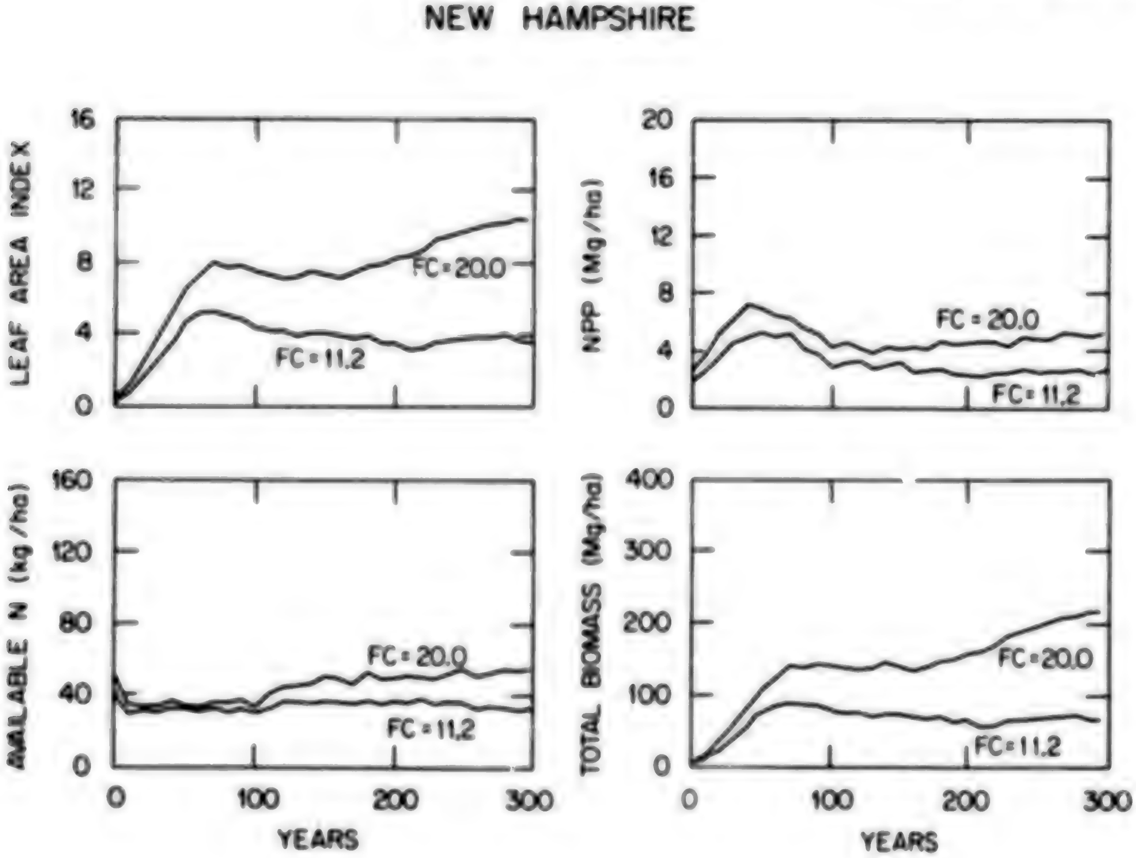
Nitrogen availabilities diverged with time, more so in New Hampshire than in North Carolina. This can be attributed to the effects of soil water capacity on species composition. In New Hampshire, the proportion of drought sensitive sugar maple was much less and the proportion of coniferous species much greater on the sandy loam compared with the silt loam (Fig. 3). This results in a shift in litter quality from easily decomposable, high N sugar maple litter to more recalcitrant, low N conifer litter, and thus N mineralization is depressed (Pastor and Post 1986). During the first 100 years of succession, both soil types are dominated by aspen and birch, and thus differences in litter quality were not great. In North Carolina, late successional communities were not greatly different on the two soil types (Fig. 4), and so differences in litter quality and N mineralization were not pronounced.

The simulated leaf area indices and biomass on both soils in New Hampshire bracket values reported for a 110 year old stand at Hubbard Brook (see compilations in Cole and Rapp 1981 and DeAngelis et at. 1981 for Hubbard Brook and Coweeta ecosystem properties). Early successional trends of pin cherry

Table 1. Comparison of regional climatic attributes with those measured at Hubbard Brook (Federer 1973, Likens et al. 1977, DeAngelis et al. 1981) and Coweeta (Johnson and Swank 1973, DeAngelis et al. 1981, updated by J. Waide, pers, comm.).

	North Carolina (Southern Mountains)	Coweeta
Precipitation (cm)	139	182
Mean January T (C)	4.2	3.2
Mean July T (C)	22.8	21.6
AET (cm)	70.0	77.5
Length of growing season (days)	168	150
	New Hampshire (South)	Hubbard Brook
Precipitation (cm)	109	130
Mean January T (C)	-9.0	-12.0
Mean July T (C)	18.7	19.0
AET (cm)	53.0	49.0
Length of growing season (days)	113	110

ORNL-DWG 86-1422



NEW HAMPSHIRE

Fig. 1. Simulated ecosystem properties for soils of two field moisture capacities in southern New Hampshire.

BEST COPY AVAILABLE

ORNL-DWG 86-1423

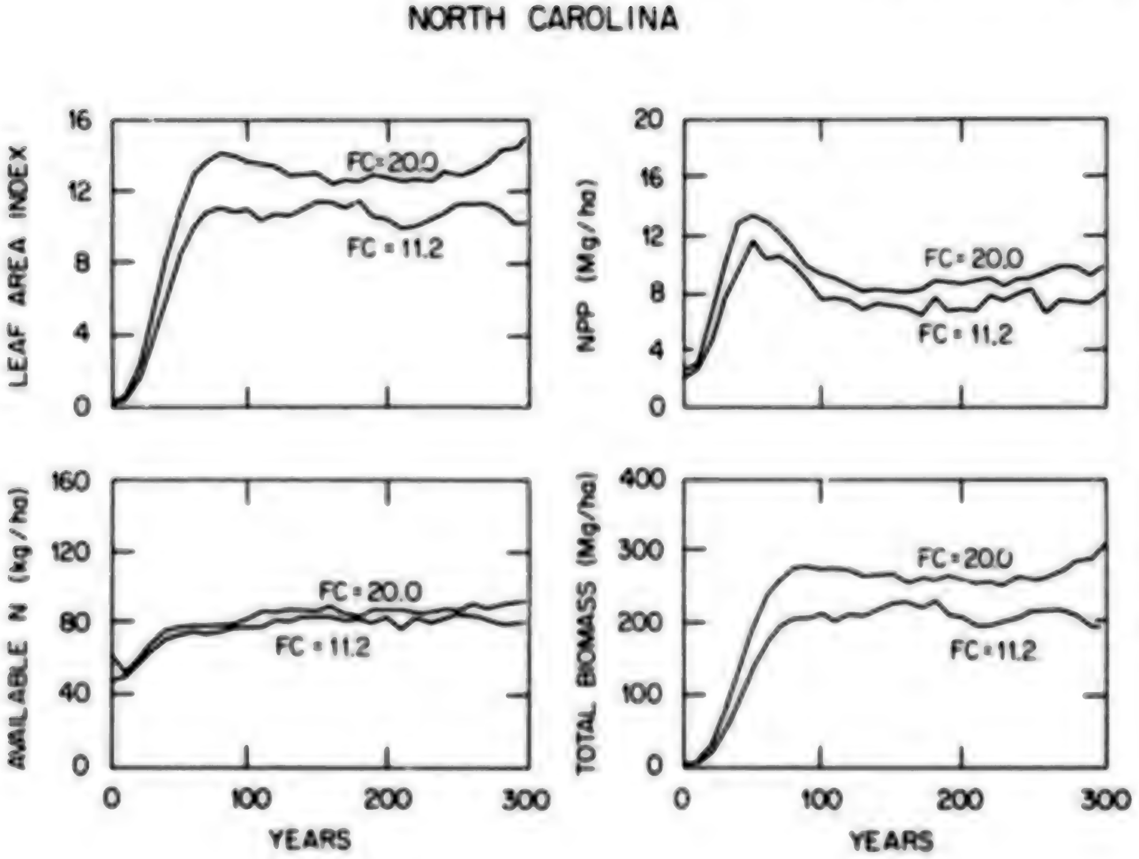


Fig. 2. Simulated ecosystem properties for soils of two field moisture capacities in southern North Carolina.

BEST COPY AVAILABLE

ORNL-DWG 86-1420

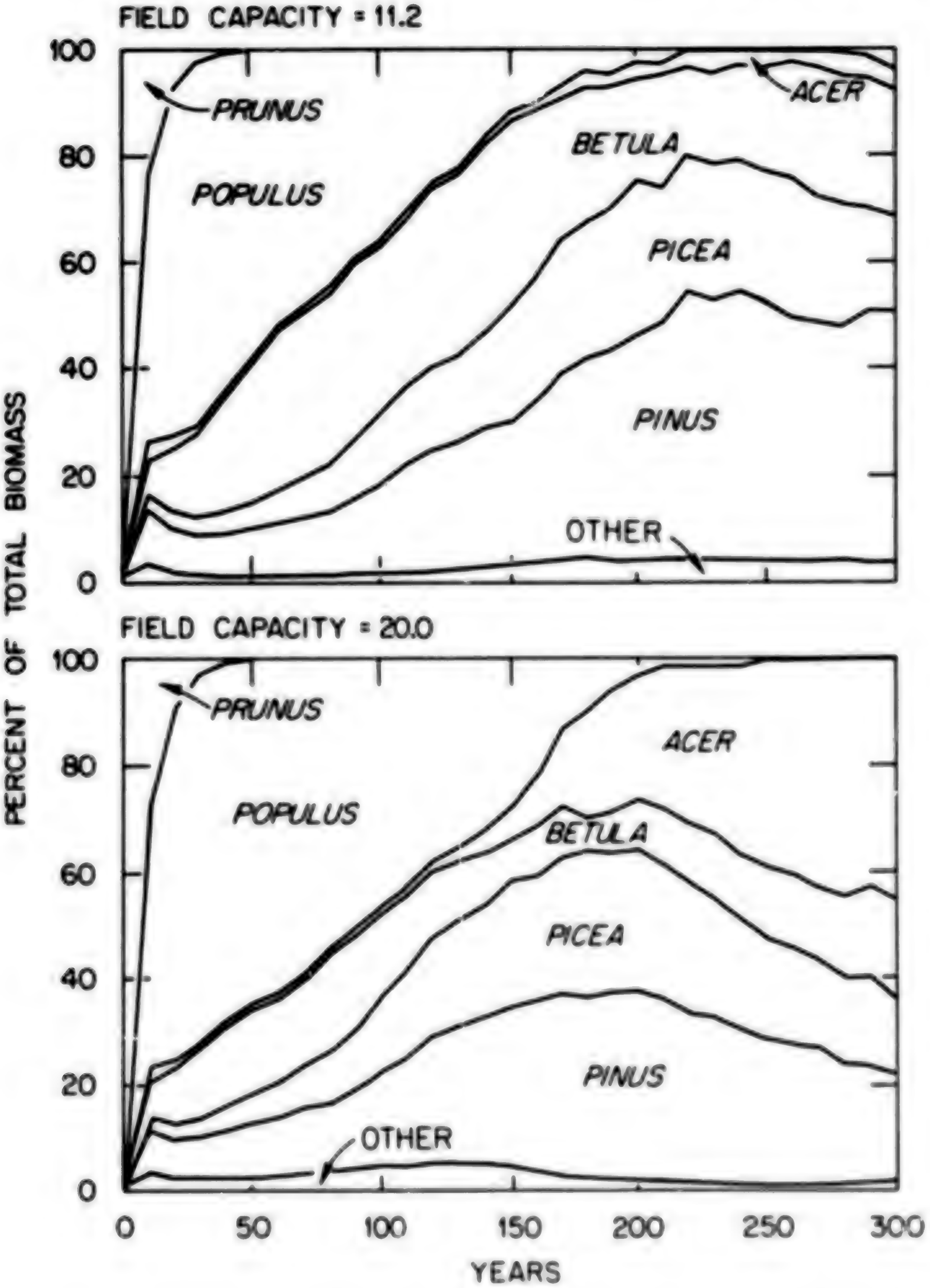


Fig. 3. Simulated species change during succession in southern New Hampshire.

BEST COPY AVAILABLE

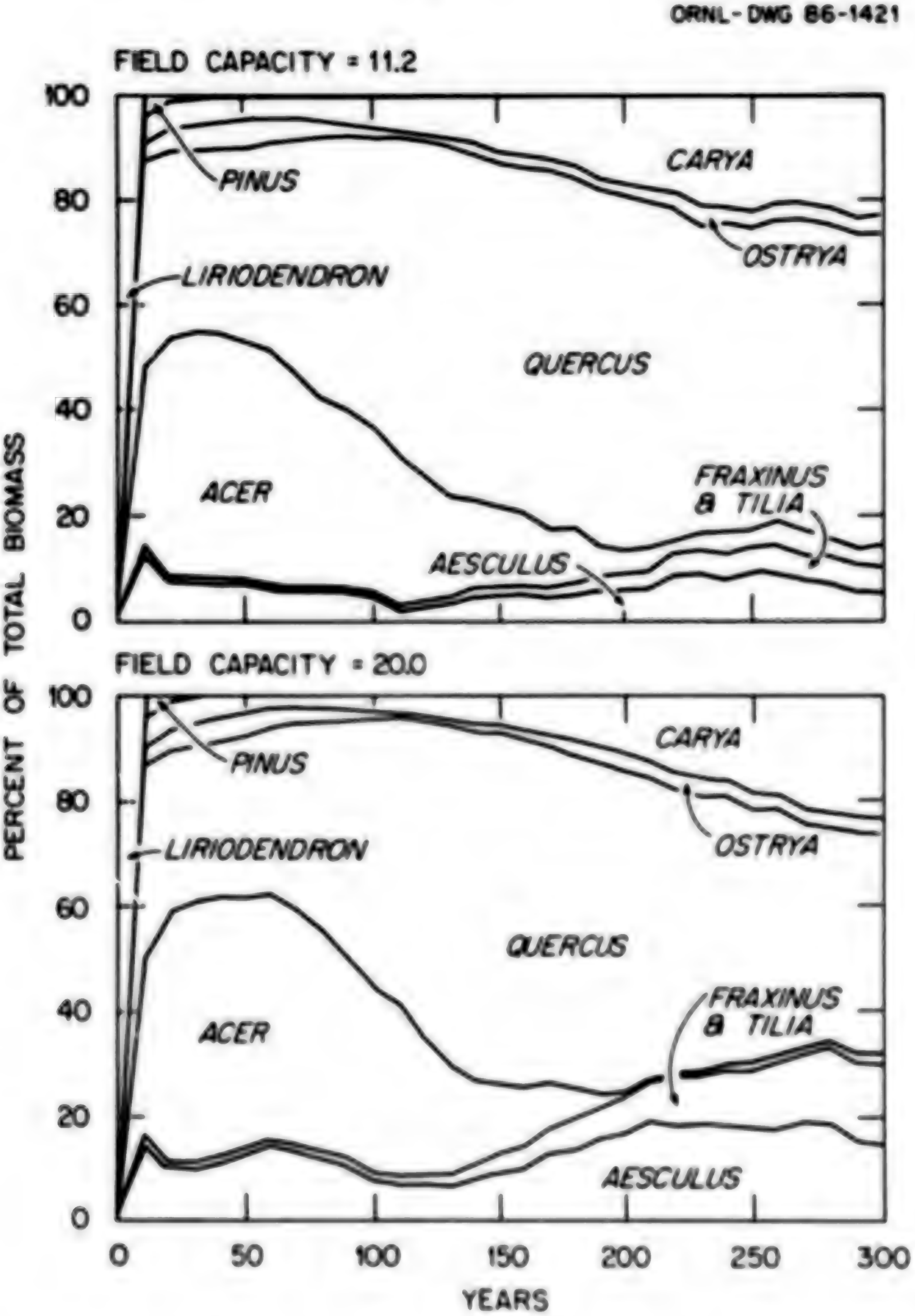


Fig. 4. Simulated species change during succession in southwestern North Carolina.

BEST COPY AVAILABLE

dominance for 20 years followed by aspen-birch dominance until year 100-120 agree favorably with that found by Marks (1974). However, simulated late successional stands have a greater conifer component, particularly pines, than currently exits at Hubbard Brook (Bormann et al. 1970). This disparity may be due to the 18th and 19th century cutting of pines throughout New England, leaving no seed source near Hubbard Brook, even though the climate is near optimum for the growth of white pine (Fowells 1965). Perhaps partly as a result of this discrepancy between simulated and actual species composition, simulated nitrogen availability and net primary production are lower than measured at Hubbard Brook (Bormann et al. 1977, Cole and Rapp 1981).

Simulated net primary production in the North Carolina runs bracket levels reported for a 60 to 200 year old oak-hickory-red maple forest at Coweeta (Cole and Rapp 1981). Leaf area was not measured in this stand. Simulated biomass of 150 to 200 Mg/ha at age 60 was slightly greater than the 137.5 Mg/ha measured (Cole and Rapp 1981). The disparity may be due to the cutting of large trees in the Coweeta watershed 60 to 80 years ago (Johnson and Swank 1973). Simulated biomass leveled off at around 200 to 260 Mg/ha by year 100. Species composition and successional trends (Fig. 4) are similar to that reported for hardwood forests in the southern Appalachians (Day 1974). Nitrogen mineralization has not been measured at Coweeta, but simulated N mineralization can be approximated as N uptake plus leaching losses minus precipitation inputs. A figure of 84.5 kg $ha^{-1} \cdot yr^{-1}$ measured at Coweeta (Cole and Rapp 1981) compares favorably with the 80 $kg \cdot ha^{-1} \cdot yr^{-1}$ simulated by year 60.

CONCLUSIONS

The model runs indicate strong interactions between soil water availability and climate in determining ecosystem properties. Properties more easily sensed by satellites, such as leaf area, were more sensitive to soil moisture than properties less easily sensed, such as soil nitrogen availability. Nevertheless, as shown in the New Hampshire runs as well as by Pastor and Post (1986) for Wisconsin and Michigan, soil nitrogen availability can be affected by soil moisture insofar as the latter affects the distribution of species, and hence the array of litter types, in the landscape. Because of feedbacks within ecosystems, particularly with regard to linked carbon-nutrient cycles, there are not proportional changes in all ecosystem properties along soil moisture and climatic gradients. If satellites can sense bands which can be calibrated against certain canopy properties (N content, lignin content, etc.), then a stronger link can be made between simulations of models, such as reported here, and remotely sensed data. Perhaps the greenness index of Tucker et al. (1985), so strongly correlated with green leaf biomass in African forests and savannahs, might prove to be correlated with some property of leaf litter important to decomposition.

Data on monthly temperature and precipitation, soil field moisture capacity and wilting point, latitude, length of growing season, and soil carbon and nitrogen content are needed in this model to simulate site carbon and nitrogen cycles. The model should also be constrained by historical land use patterns to the best of our knowledge, since many of these may have affected species composition (e.g., selective cutting) or soil thickness and organic matter content (e.g., erosion). For example, Pastor and Post (1986) found a wide variety of patterns of soil organic matter recovery after disturbance predicted by this model and partially validated in the field depending on initial soil organic matter content and early successional species composition. Thus, land use patterns superimposed on nested soil water-climatic gradients introduce more variability in the landscape and, therefore, more uncertainty in regional estimation of ecosystem properties. It is probable that the degree of variability due to past land use depends not only on type of practice, but also time and a three way land use-soil moisture-climate interaction.

We are still far from answering these questions and developing methods of regional estimation of ecosystem properties from detailed site studies and remotely sensed data. Still, it was only 15 years ago that the original version of this model was introduced for New England (Botkin et al. 1972). The original JABOWA model considered soil-vegetation interactions only in a crude way. In the past 15 years, the model has been expanded until in its present form it approaches a general ecosystem model of upland eastern North American forests. It remains to be seen whether wetland forest ecosystems function according to the general paradigm of nested soil moisture-climatic gradients. In conjunction with site-specific ground and satellite monitoring and inventories of the current areal extent of various ecosystems (Olson et al. 1983, Emanuel et al. 1985), the model may assist in formalizing a general paradigm of landscape, regional, and global ecology.

ACKNOWLEDGMENTS

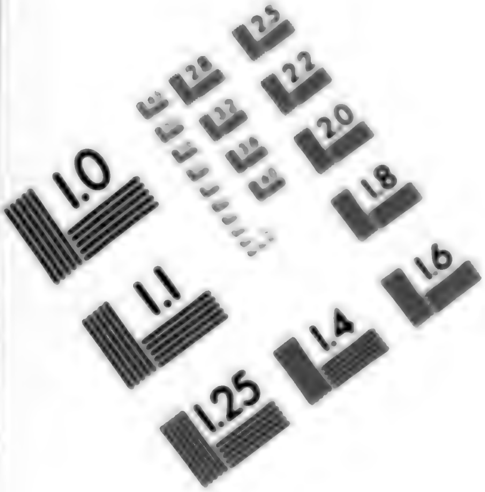
Research supported by the Department of Energy's Global Carbon Cycle Program under Contract No. DE-AC05-840R21400 with Martin Marietta Energy Systems. Inc., and by a Wigner Fellowship to MH. JP was an Oak Ridge Associated Universities Postdoctoral Fellow in the Environmental Sciences Division during this research: the assistance of this organization is greatly appreciated. Publication No. 2729, Environmental Sciences Division. Oak Ridge National Laboratory.

LITERATURE CITED

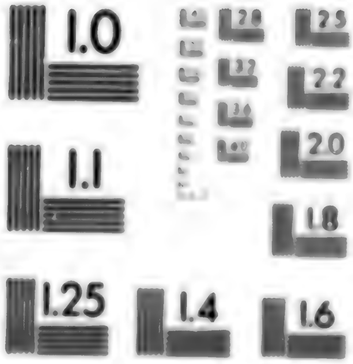
Aber, J.D., J.M. Melillo, and C.A. Federer. 1982. Predicting the effects of rotation length, harvest intensity, and fertilization on fiber yield from northern hardwood forests in New England. Forest Science 28: 31-45.

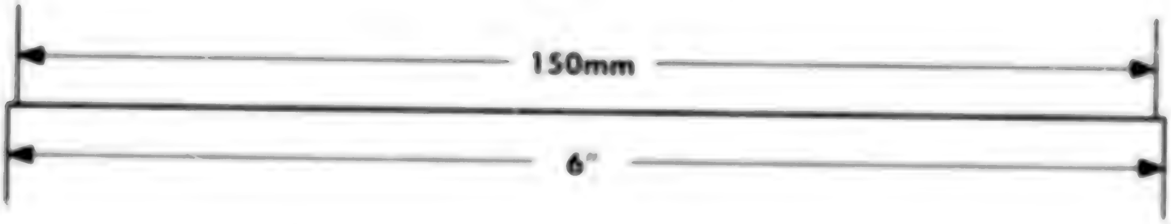
Basset, J.R. 1964. Tree growth as affected by soil moisture availability. Proceedings, Soil Science Society of America 28: 436-438.

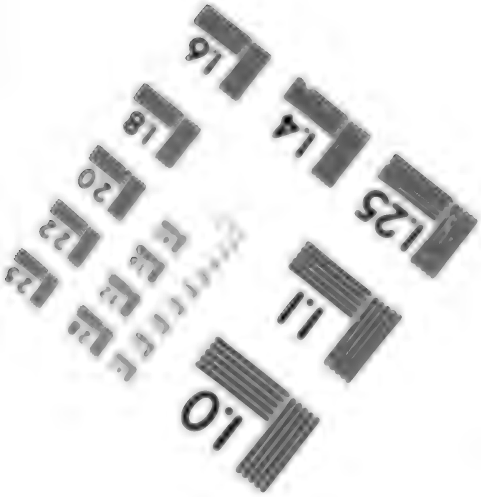
Bormann, F.H., T.G. Siccama, G.E. Likens, And R.H. Whittaker. 1970. The Hubbard Brook ecosystem study: Composition and dynamics of the tree stratum. Ecological Monographs 40: 377-388.

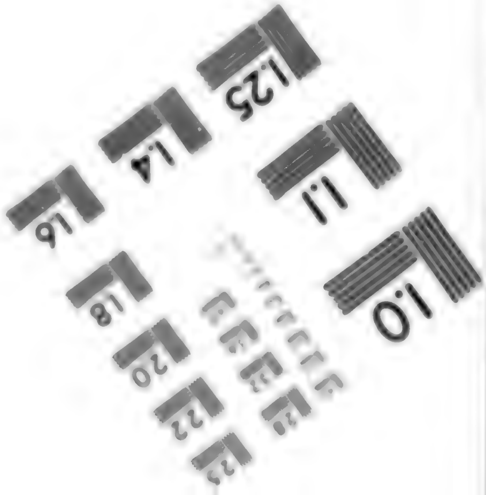


UNITED STATES OF AMERICA
GOVERNMENT PRINTING OFFICE









Bormann, F.H., G. E. Likens, and J.M. Melillo. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. Science 196:981-983.

Bormann, F.H., and G.E. Likens. 1979. Pattern and process in a forest ecosystem. Springer-Verlag, New York.

Botkin, D.B. 1981. Causality and succession. Pages 36-55 in D.C. West, H.H. Shugart, and D.B. Botkin (editors), Forest Succession. Springer-Verlag, New York.

Botkin, D.B., J.F. Janak, and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60:849-872.

Bourdeau, P. 1954. Oak seedling ecology determining segregation of species in Piedmont oak-hickory forests. Ecological Monographs 24:297-320.

Cole, D.W. and M. Rapp. 1981. Element cycling in forest ecosystems. Pages 341-410 in D.E. Reichle (editor), Dynamic Properties of Forest Ecosystems. IBP 23. Cambridge University Press, Cambridge.

Day, F.P. 1974. Primary production and nutrient pools in the vegetation of a southern Appalachian watershed. Ph.D. dissertation, University of Georgia, Athens.

DeAngelis, D.L., R.H. Gardner, and H.H. Shugart. 1981. Productivity of forest ecosystems studied during IBP: The woodlands data set. Pages 567-672 in D.E. Reichle (editor), Dynamic Properties of Forest Ecosystems. Cambridge University Press, Cambridge.

Emanuel, W.R., H.H. Shugart, and M.P. Stevenson. 1985. Climatic change and the broad scale distribution of terrestrial ecosystem complexes. Climatic Change 7:29-43.

Federer, C.A. 1973. Annual cycles of soil and water temperatures at Hubbard Brook. USDA Forest Service Research Note NE-167.

Fowells, H.A. (editor). 1965. Silvics of forest trees of the United States. USDA Forest Service, Agricultural Handbook 271.

Johnson, P.L. and W.T. Swank. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. Ecology 54:70-80.

Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton, and N.M. Johnson. 1977. Biogeochemistry of a forested ecosystem. Springer-Verlag, New York.

Mann, L.K. and W.M. Post. 1980. Modeling the effect of drought on forest growth and composition. Bulletin of the Ecological Society of America 61:80.

Marks, P.L. 1974. The role of pin cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44:73-88.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465-472.

Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621-626.

Mitchell, H.L. and R.F. Chandler. 1939. The nitrogen nutrition and growth of certain deciduous trees of northeastern United States. Black Rock Forest Bulletin No. 11.

Monk, C.D. 1966. An ecological significance of evergreenness. Ecology 47:504-505.

Monsi, M., Z. Uchijima, and T. Oikawa. 1973. Structure of foliage canopies and photosynthesis. Annual Review of Ecology and Systematics 4:301-328.

Olson, J.S., J.A. Watts, and L.J. Allison. 1983. Carbon in live vegetation of major world ecosystems. ORNL Report ORNL-5862, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Pastor, J., J.D. Aber, C.A. McClaugherty, and J.M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256-268.

Pastor, J. and W.M. Post. 1985. Development of a linked forest productivity-soil process model. ORNL/TM-9519.

Pastor, J. and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry (in press).

Shugart, H.H. 1984. A theory of forest dynamics. Springer-Verlag, New York.

Shugart, H.H. and D.C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. Journal of Environmental Management 5:161-179.

Solomon, A.M., M.L. Tharp, D.C. West, G.E. Taylor, J.W. Webb, and J.L. Trimble. 1984. Response of unmanaged forests to CO-2-induced climatic change: Available information, initial tests, and data requirements. USDOE, Office of Energy Research, CO2 research Division, Washington, D.C. DOE/NBB-0053-TR009.

Tucker, C.J., J.R.G. Townsend, and T.E. Goff. 1985. African land cover classification using satellite data. Science 227:369-375.

United States Department of Commerce. 1968. Climatic atlas of the United States. Superintendent of Documents, Washington, DC.

United States Department of Commerce. 1982. Monthly averages of temperature and precipitation for state climatic divisions. Climatography of the United States. National Climatic Center, Asheville, North Carolina.

Van Cleve, K., L. Oliver, R. Schlentner, L. Viereck, and C.T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research 13:747-766.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Whittaker, R.H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103-121.

Whittaker, R.H., G.E. Likens, F.H. Bormann, J.S. Eaton, and T.G. Siccama. 1979. The Hubbard Brook ecosystem study: Forest nutrient cycling and element behavior. Ecology 60:203-220.

CHAPTER 9. NORTH AMERICAN VEGETATION PATTERNS OBSERVED WITH METEOROLOGICAL SATELLITE DATA[1]

SAMUEL N. GOWARD[2], COMPTON J. TUCKER, AND DENNIS G. DYE[2]
Code 623, NASA/Goddard Space Flight Center
Greenbelt, Maryland 20771

Abstract. Results from analysis of North American polar-orbiting meterological satellite observations, extending from April to November 1982, show that the satellite data correspond to the known seasonality of North American natural and cultivated vegetation. Integration of the observations over the growing season produced measurements that are related to primary productivity patterns of the major North American natural vegetation formations. Regions of intense cultivation were observed as anomalous areas in the integrated growing season measurements. These anomalies can be explained by contrasts between cultivation practices and natural vegetation phenology. Information on seasonality, extent and interannual variability of vegetation photosynthetic activity at continental scales can be derived from these satellite observations.

INTRODUCTION

Information concerning the distribution and seasonality of global vegetation has been derived from a wide range of information sources, such as maps, atlases, and field reports. Often these sources are of varying reliability, and usually are compiled from observations taken at different times. Recent efforts to estimate the global extent of selected vegetation types have produced results which differ by more than a factor of two for comparable vegetation types (Atjay et al. 1979, Olson and Watts 1982). Much less information is available on the global patterns of vegetation seasonality (Junge and Czeplak 1968, Lieth 1974, Fung et al. 1983). There is, therefore, a need for consistent, timely and reliable information about global vegetation patterns. Remotely sensed measurements of reflected solar radiation can provide such an information source. We discuss preliminary results of a study of North American vegetation patterns observed with visible and near-infrared measurements from the NOAA-7 Advanced Very High Resolution Radiometer (AVHRR).

[1] This is adapted from a paper published in Vegetatio, Vol. 64, pp. 3-14 (1985).

[2] Also with the Department of Geography, University of Maryland, College Park, Maryland 20742.

BACKGROUND

Spectral Vegetation Indices

Research carried out since the 1940s has shown that photosynthetically active 'green' vegetation displays a unique spectral reflectance pattern in the visible and near-infrared spectral regions when compared to other earth surface materials (Krinov 1947, Colwell 1956, Gates et al. 1965, Knipling 1970). The spectral reflectance of rocks, soils, dormant vegetation, and woody plant materials, although variable in overall brightness, generally increases monotonically with increasing wavelength in the 0.4 to 1.0 μm wavelength region. Photosynthetically active plant components, primarily leaves, produce a stepped reflectance pattern, with low reflectance in the visible, and high reflectance in the near infrared. This complex green vegetation spectral reflectance pattern results from scattering with strong absorption of visible light by chlorophylls and related pigments, and scattering with little absorption, because of leaf structural properties, and minimal absorption of light in the near infrared. Researchers have proposed a number of spectral vegetation indices based on the premise that there are contrasts in spectral reflectance between green vegetation and background materials (Pearson and Miller 1972, Rouse et al. 1974, Kauth and Thomas 1976, Richardson and Wiegand 1977, Tucker 1979, Holben et al. 1980; Curran 1983, Jackson 1983). All of the indices are computed, at least in part, by calculating a difference or ratio of visible to near-infrared measurements. This calculation minimizes the effects of variable background brightness, while emphasizing variations in the measurements that occur because of varying green vegetation density. The normalized difference vegetation index (NDVI) is representative of the various spectral vegetation indices. It is computed:

$$\mathrm{NDVI} = (\mathrm{NIR}-\mathrm{VIS})/(\mathrm{NIR}+\mathrm{VIS}) \qquad (1)$$

where NIR = near-infrared spectral measurement

VIS = visible spectral measurement

In theory, NDVI measurements range between -1.0 and +1.0. However, in practice the measurements generally range between -0.1 and +0.7. Clouds, water, snow, and ice give negative NDVI values. Bare soils and other background materials produce NDVI values between -0.1 and +0.1. Larger NDVI values occur as the amount of green vegetation in the observed area increases. However, analytical evaluation has shown that the various indices are functional equivalents (Perry and Lautenschlager 1984).

Recent field studies of several different agricultural crops have shown a strong linear relation between the intercepted photosynthetically active radiation (IPAR) and the spectral vegetation indices (Kumar and Monteith 1982, Daughtry et al. 1982, Hatfield et al. 1983, Asrar et al. 1984). This IPAR-spectral vegetation index relation provides a physical link between the indices and plant productivity (Sellers 1985). Support is lent by studies of crops and grasslands that show a direct relation between the integrated value of spectral vegetation index measurements, acquired several times through the growing season, and the seasonal accumulation of dry matter (Tucker et al. 1981; Hatfield 1983, Steven et al. 1983, Tucker et al. 1985b). This research suggests that periodic visible and near-infrared observations of the earth may be used to characterize the current status, seasonal dynamics, and integrated seasonal magnitude of vegetation photosynthetic activity.

Advanced Very High Resolution Radiometer

Satellite-based remote sensing observations provide data for vegetation studies of all land areas conveniently, consistently, and repeatedly. Much attention has been given to LANDSAT multispectral scanner (MSS) observations, and selected studies have successfully used these measurements to analyze the regional extent, seasonality, and productivity of natural and cultivated vegetation (Dethier 1974, Deering et al. 1975, NASA/JSC 1979, Thompson and Wehmanen 1979). However, LANDSAT data are not well suited for global scale studies. The MSS 80-meter ground resolution produces a large data volume--over 6,000 MSS scenes are required for one observation of the earth's total land area--and in cloudy regions of the globe, the 18-day repeat cycle produces too few cloud-free observations to record vegetation seasonal dynamics. The AVHRR sensor on the TIROS-N series of meteorological satellites, beginning with NOAA-6 launched in 1979, provides an alternate source of satellite visible and near-infrared measurements. With a 1.1-km and ∿4-km nadir ground resolutions and a daily repeat cycle, the AVHRR observations are well suited for large area studies. Several researchers have begun to use this new source of spectral measurements in vegetation studies, and the results are encouraging (Townshend and Tucker 1981; Gray and McCrary 1981; Greegor and Norwine 1981; Ormsby 1982; Justice 1983; Tucker et al. 1985a,b; Justice et al. 1985, Norwine and Greegor 1983).

The AVHRR is a multispectral imaging sensor that was designed to permit detection and discrimination between clouds, land, water, snow, and ice (Schneider and McGinnis 1977). Spectral measurements are acquired in the visible, near infrared, middle infrared, and thermal infrared regions, with four channels on the earlier AVHRR instruments on TIROS-N and NOAA-6 satellites and five channels on NOAA-7, NOAA-8, and NOAA-9 (Table 1). AVHRR observations are available from the U.S. National Oceanic and Atmospheric Administration (NOAA) in several forms, including high resolution picture transmission (HRPT), local area coverage (LAC), global area coverage (GAC), and global vegetation index (GVI) (Kidwell 1979). The HRPT data are direct transmission data to ground receiving stations. The LAC data are the original 1.1 km observations, which are only recorded and placed in archives on special request. The GAC data, which are regularly recorded and stored, are partially resampled LAC observations. GAC data are produced by calculating the average value of the first four pixels in a 3 x 5 array of LAC observations. The average value is then used to represent the 3 x 5 pixel area.

Table 1. Characteristics of the NOAA/AVHRR system

TIROS-N - launched Oct. 1978 - Protoflight NASA funded

NOAA-6 - launched June 1979 - NOAA funded

NOAA-7 - launched June 1981 - NOAA funded

NOAA-8 - launched March 1983 - NOAA funded

Coverage Cycle	9 days	Orbit Inclination	102°
Scan Angle Range	+ 56°	Orbital Flight	850 km
Ground Coverage	2700 km	Orbital Period	102 mins

IFOV	1.39-1.51 mr	Equatorial Crossing	Des.	Asc.
			0730 /	1930 (NOAA 6 & 8)
Ground Resolution	1.1 km (nadir) 3.5 km (max off angle)		1430 /	0230 (NOAA 7)
Quantization	10 bit			

Spectral Channels	1	2	3	4	5
Spectral Range (µm)	0.58-0.68[a]	0.725-1.1	3.55-3.93	10.3-11.2	11.5-12.5[b]

---

[a] Channel 1 range on TIROS-N 0.55-0.90.

[b] Not on NOAA 6.

DATA AND METHODS

Two aspects of the North American AVHRR NDVI measurements are examined in this study; (1) seasonal vaiability and (2) growing-season summation or integral with respect to time. The seasonal variations are related to the phenology of vegetation and the absorbed photosynthetically active radiation. The integral of these measurements over the growing season is related to annual primary productivity (Monteith 1977). However, these relations have not previously been examined across the diversity of vegetation types encountered in North America.

AVHRR data were selected for this study, and observations from NOAA-7 were used because the nominal daylight overpass time is 1430 hours, compared to 0730 hours for NOAA-6 and NOAA-8. The analysis presented here examines observations from April to November of 1982. Inspection of the winter (November to March) North American observations reveals that low irradiance measurements at extreme latitudes can give spurious NDVI values. Restricting the current analysis to April through November avoids this problem, while capturing the majority of the North American growing season north of 35°N. Along the central west coast of the continent the full growing season is not observed in this analysis.

Three-week Composites

Thirty weeks of AVHRR data, extending from 12 April 1982 to 7 November 1982, were processed to form 10 three-week composites (after Holben and Fraser 1984). Examples of the three-week composites for April, June, August, and October are provided in Fig. 1. The NDVI value at each grid cell location is color-coded, dependent on its magnitude, as shown by the color bar in Fig. 1. The same color code is used for all the maps to permit interseasonal comparisons. A latitude-longitude coordinate grid, national boundaries, and state boundaries in the United States are superimposed on the image to aid interpretation.

Integrated NDVI Measurements

The area under the temporal curve was computed by trapezoidal integration of the three-week interval composite values at each grid cell location on the map. These resultant measurements are displayed in Fig. 2. The same color code used in Fig. 1 is used here with the exception that each value is multiplied by ten. These measurements are referred to as integrated NDVI values.

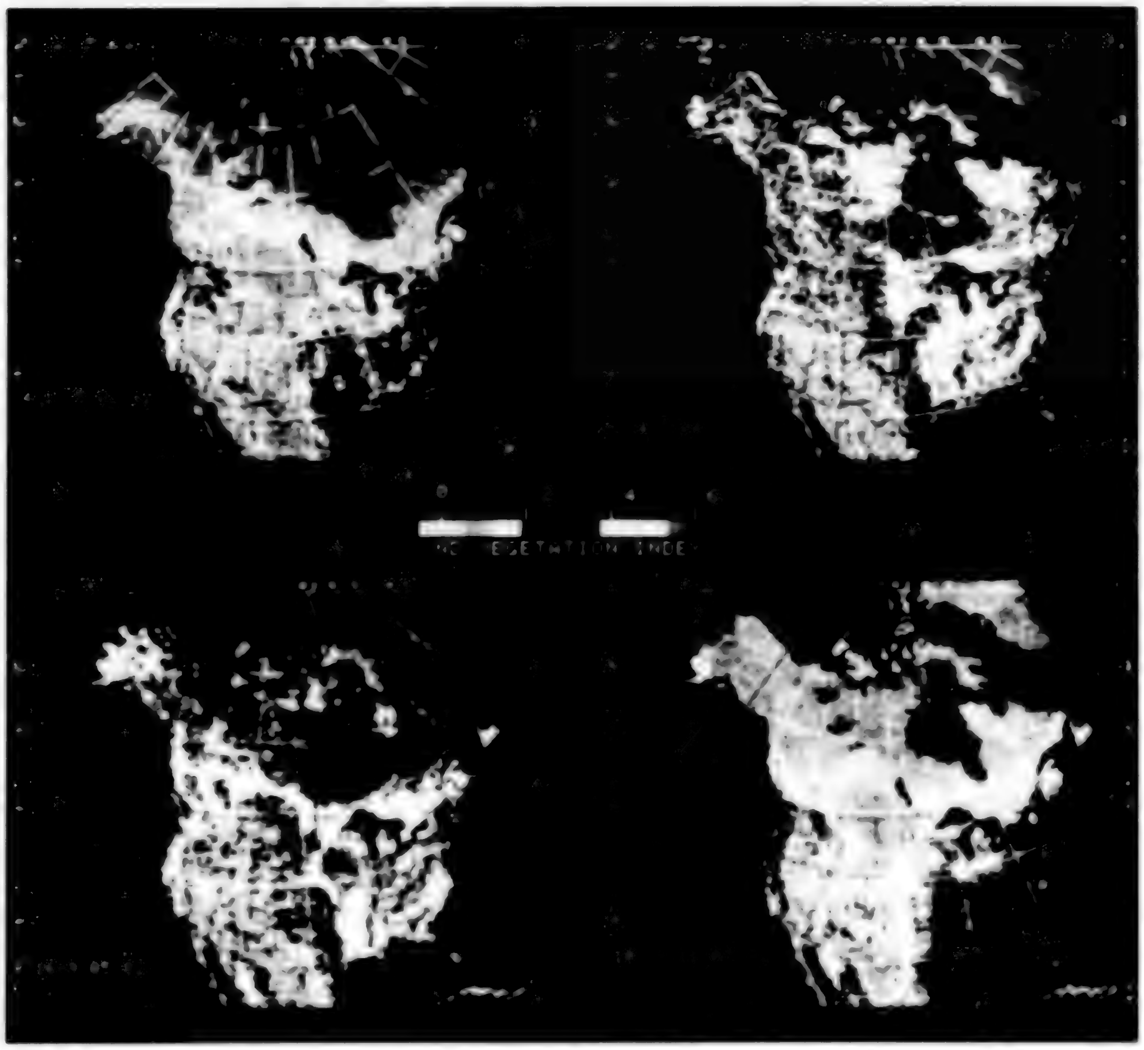


Fig. 1. Three-week composite maps of North American normalized difference vegetation index measurements for April, June, August, and October 1982. The measurements are color-coded dependent on magnitude as displayed on the color bar in the center of the figure.

BEST COPY AVAILABLE

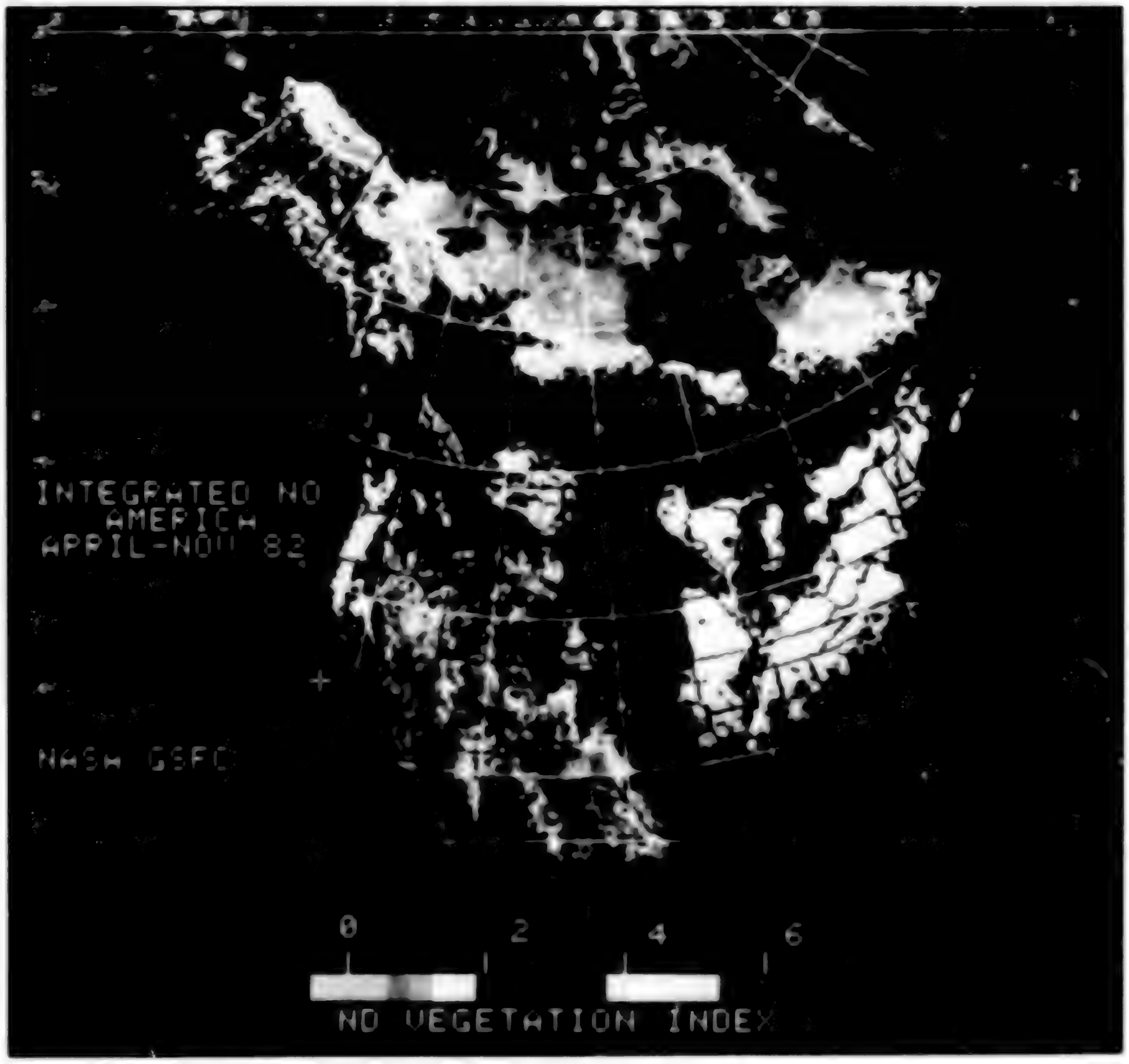


Fig. 2. Map of NDVI measurements integrated over the April to November 1982 observation period. The integration was computed by trapezoidal approximation of the area under the curve subtended by the 10 three-week composite NDVI measurements. The ∫NDVI measurements are displayed with a color code equivalent to that used in Fig. 1, except that the numerical values are ten times larger.

BEST COPY AVAILABLE

RESULTS AND DISCUSSION

Seasonal NDVI Patterns

The three-week composites (Fig. 1) show that in general the NDVI measurements increase to a maximum in late August and thereafter decline. This seasonality is in agreement with the phenology of North American vegetation (Lieth 1974). High NDVI values move northward across the continent in the spring and summer and shift to the South in the fall. This green-wave and brown-wave phenomenon has previously been studied for selected regions of the continent with LANDSAT observations where it has been related to the seasonal pulse of photosynthetic activity in the vegetation present (Dethier 1974, Blair and Baumgardner 1977).

The seasonal variations of NDVI measurements for regions of selected natural and cultivated vegetation types are presented in Fig. 3. These plots are the average of a 3 x 3 array of GVI three-week composite measurements centered on the locations given. The observations are primarily from land dominated by natural vegetation, although the effects of human activities in these locations cannot be entirely overlooked (e.g., irrigated agriculture). The plots in Fig. 3a are for locations where the seven months of AVHRR observations cover the majority of the growing season. The Lovelock, Nevada, observations of desert conditions are provided for comparison. As previously noted, the measurements increase in the spring and decline in the fall. The magnitude of the summer measurements in general decreases with increasing latitude. Also, the duration of high summer values decreases to the North. However, grassland observations from Nebraska peak at lower summer values than for the boreal coniferous forest, but with a longer duration of elevated values. These trends in the NDVI measurements correspond with the observed phenological patterns of these vegetation formations (Lieth 1974).

The plots in Fig. 3b are for regions of the continent where the full growing season is not observed in this seven-month period. The NDVI plots for both Oregon and California show high NDVI measurements in April, suggesting a continuation of vegetation activity from the winter months. The California NDVI levels decline steadily throughout the observation period, which agrees with the increased vegetation dormancy observed in this region through the arid summer. The Oregon observations remain at high values until September and thereafter decline, reflecting the more humid character of this region as well as the physiology of these coniferous forests (Waring and Franklin 1979). The South Carolina observations, from a region of pine forests, show a spring increase in the NDVI measurements and a small decline in the fall, suggesting continued photosynthetic activity in the winter. No simple explanation of the mid summer decline in NDVI values in South Carolina can be given. Several possibilities, including drought conditions in this region during 1982, cloud cover contamination, and atmospheric water vapor effects, may explain or contribute to an explanation of this pattern.

Representative temporal plots of NDVI measurements from prime agricultural regions are presented in Fig. 3c. Both the corn-soybean and spring

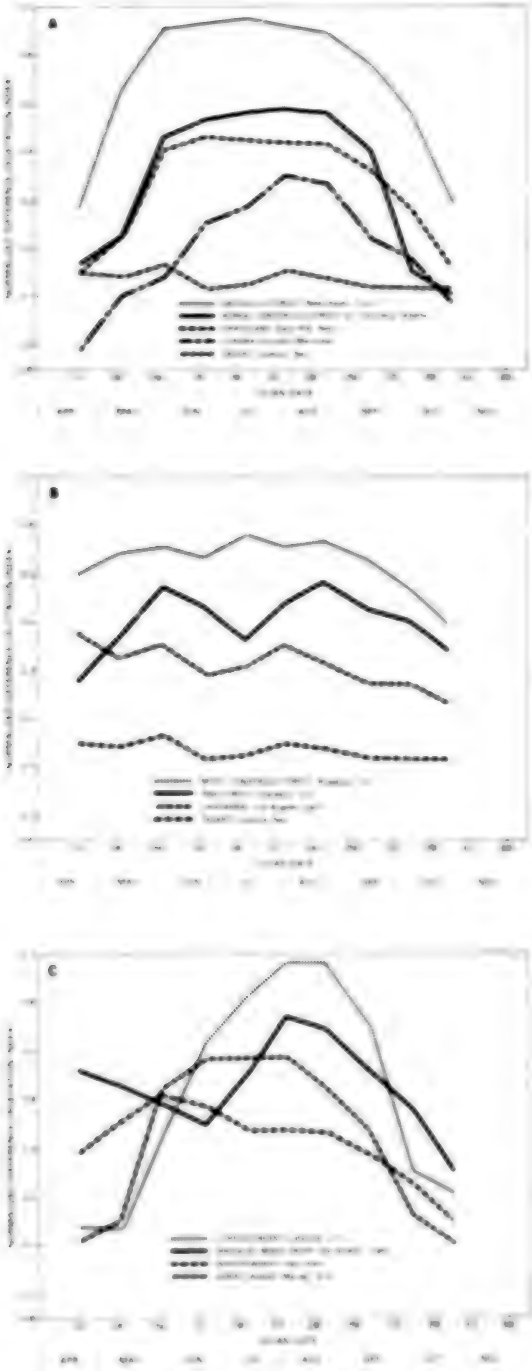


Fig. 3. Temporal variations of the normalized difference vegetation index measurements for selected sites of natural and cultivated vegetation types. Vegetation-type identification was by means of maps presented in Fig. 5 and Fig. 6. The plotted measurements are the mean of a 3 x 3 array of NDVI measurements centered on the cited locations. (a) Natural vegetation observed over the growing season, (b) natural vegetation with a growing season extending into winter months, (c) cultivated vegetation.

BEST COPY AVAILABLE

wheat regions green up later and senesce (and/or are harvested) earlier than local natural vegetation. The winter wheat observations show high values in April, with a peak in June and declining values thereafter. The California Central Valley observations are high in April and decline until early July when they again increase to a maximum in late August. These temporal patterns are related to the calendar of cultivation and growth of crops, which differs from natural vegetation phenology. This differential timing between cultivated and natural vegetation growth can also be observed in the three-week composites where the prime cropland areas display distinctive patterns in the images. For example, the winter wheat region, extending from north central Texas through central Oklahoma and Kansas, stands out as an island of high NDVI values in the April image, whereas the cornbelt shows up as an area of low values in this same image.

The NDVI measurements and climatic conditions should be related if the NDVI measurements are a sensitive indication of vegetation activity (Holdridge 1947, Mather and Yashioka 1958, Odum 1971, Box 1981). The NDVI measurements, precipitation and temperature records for Point Barrow, Alaska, and Phoenix, Arizona, for the seven-month period are plotted in Fig. 4. At Point Barrow, the NDVI measurements only increase above 0.0 after mid-June, when the temperature rise above 0°C, a condition essential for vegetation growth. In the Phoenix, Arizona, region temperatures are always above freezing, but moisture limits vegetation growth. NDVI measurements for Phoenix follow moisture seasonality, showing lower values in the dry season from April to July and an increase in late summer when rainfall increases. This interaction between the NDVI measurements and climatic conditions is suggestive of the value of spectral vegetation index measurements in regional- to global-scale vegetation phenology research.

Integration Over the Growing Season

The map of integrated normalized difference vegetation index (∫NDVI) measurements (Fig. 2) displays a pattern of marked familiarity. The highest values occur in the southeastern and central west coast regions of the continent. The integrated measurements generally decrease to the North and West across North America but display more heterogeneity in the western one-third of the continent. The north-south gradient of ∫NDVI measurements corresponds to the major temperature ecocline of North America, whereas the east-west gradient corresponds to the major precipitation ecocline of the continent (Whittaker 1970). The geographic complexity of the measurements in western North America is related to the mountainous terrain of the region. Note that elevation affects the measurements differentially dependent on latitude. North of 50°N latitude, the ∫NDVI measurements decrease with increasing elevation. South of 40°N latitude the measurements increase with increasing elevation. This geography of ∫NDVI measurements compares well with the known patterns of North American natural vegetation activity (Shelford 1963, Küchler 1964, Whittaker 1970, Odum 1971, Rodin et al. 1975, Lieth 1978).

The pattern of ∫NDVI values in certain areas of the continent, particularly in the United States, appears 'anomalous' considering the natural

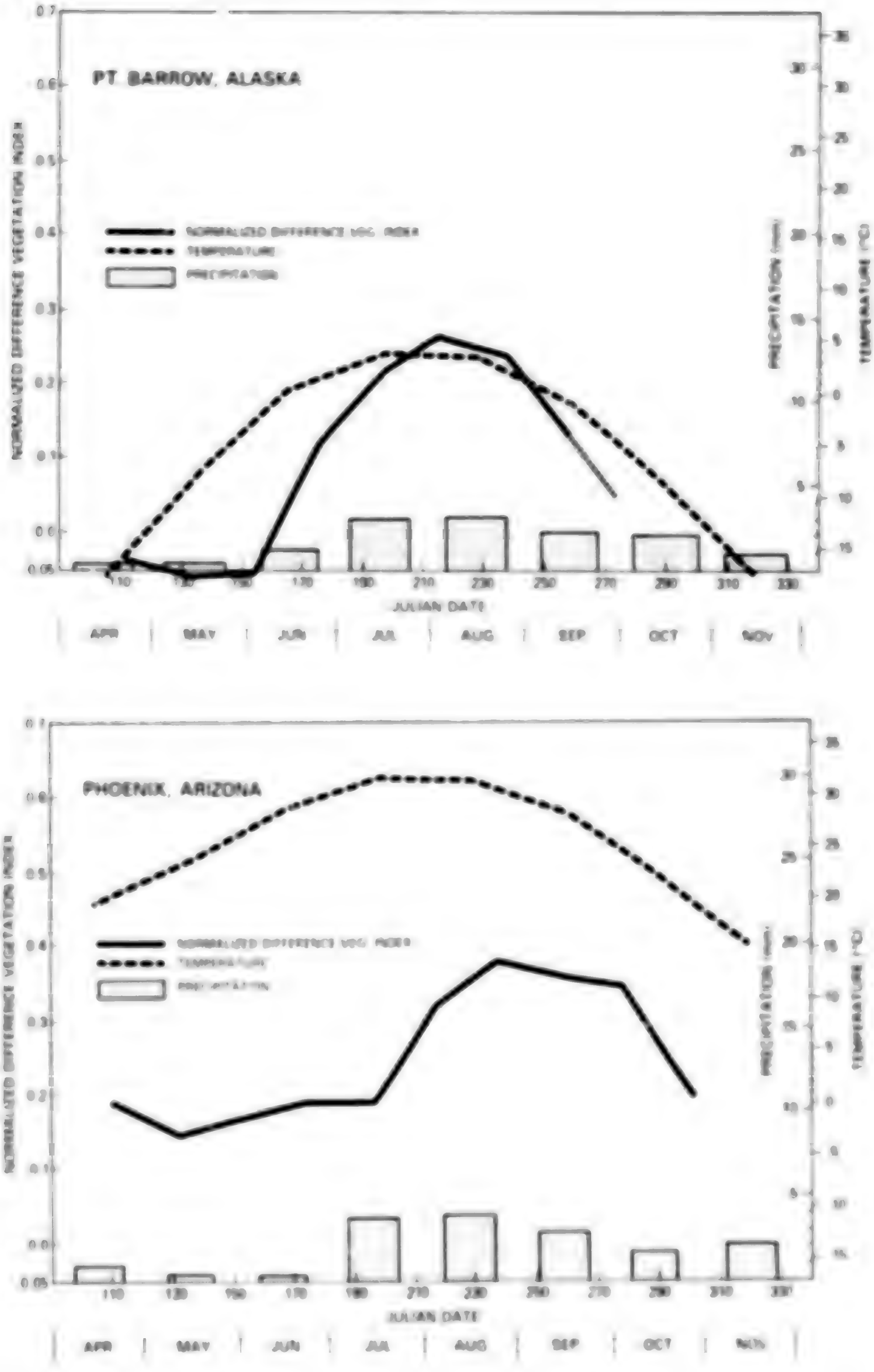


Fig. 4. Comparison of normalized difference vegetation index measurements and climate data for Point Barrow, Alaska, and Phoenix, Arizona. The NDVI measurements were computed in the same manner as those presented in Fig. 3. The climate observations are 30-year averages from the NOAA world weather station records (NOAA 1982).

BEST COPY AVAILABLE

vegetation and terrain of these locations. A region in the midwestern United States, extending from central Ohio to Iowa and including much of Indiana and Illinois, as well as portions of Wisconsin and Michigan, produce $\int$NDVI values that are lower than might at first be expected. A similar area of relatively low $\int$NDVI values extends north-south in the Mississippi River Valley from extreme southeastern Missouri through Arkansas and Tennessee to northwestern Mississippi. Conversely, selected regions in the western United States, including the Columbia and Snake River basins in the Northwest, the Central and Imperial valleys in California, and several locations in the Great Plains, exhibit higher than expected $\int$NDVI values. These locations correspond to the prime croplands in the United States (Fig. 5). The relatively low $\int$NDVI values in the U.S. Midwest occur because this region produces low NDVI values both early and late in the growing season, prior to planting and following harvest. Most agriculture in the western portion of the United States depends upon irrigation to sustain plant growth which produces greater plant cover and, thus, higher $\int$NDVI values than observed from natural vegetation of this semiarid region. These patterns correspond to the observed impact of agriculture on regional net primary productivity (Whittaker and Likens 1975).

$\int$NDVI Measurements and Net Primary Productivity

The relation between $\int$NDVI measurements and net primary productivity (NPP) was examined by computing the mean $\int$NDVI value for each of the major vegetation biomes of the continent and comparing these figures to net primary productivity figures reported in the literature. The North American biome map (Fig. 6) from Odum (1971) was used as a means to identify the natural vegetation formations. $\int$NDVI samples were selected from sites within each formation based on the location of world weather observing stations used by World Meteorological Organization for global studies (NOAA 1982). These sites were selected since they are uniformly distributed, approximately every 5° of latitude and longitude, across the continent. There are an average ten stations within each major biome. For each station the mean of a 3 x 3 pixel array of $\int$NDVI measurements, centered on the station location, was computed. The mean of all sites within each biome was then computed. These biome-averaged NDVI measurements were compared to net primary productivity figures provided by Whittaker and Likens (1975) supplemented by NPP figures for subclimax pine and pine/oak forests from Whittaker (1970) and values for the ecotones from Lieth (1978) and Rodin et al. (1975). The results (Fig. 7) show a strong direct relation between the NDVI measurements and net primary productivity. Excluding agriculture the explained variance (r^2) of the relation is 0.94. With agriculture included, the r^2 value drops to 0.89. Further investigation is required before these results are fully understood. However, the correspondence between these two variables is sufficient to suggest that satellite-derived spectral vegetation index measurements will significantly improve temperate studies of vegetation productivity in the temperate latitudes.

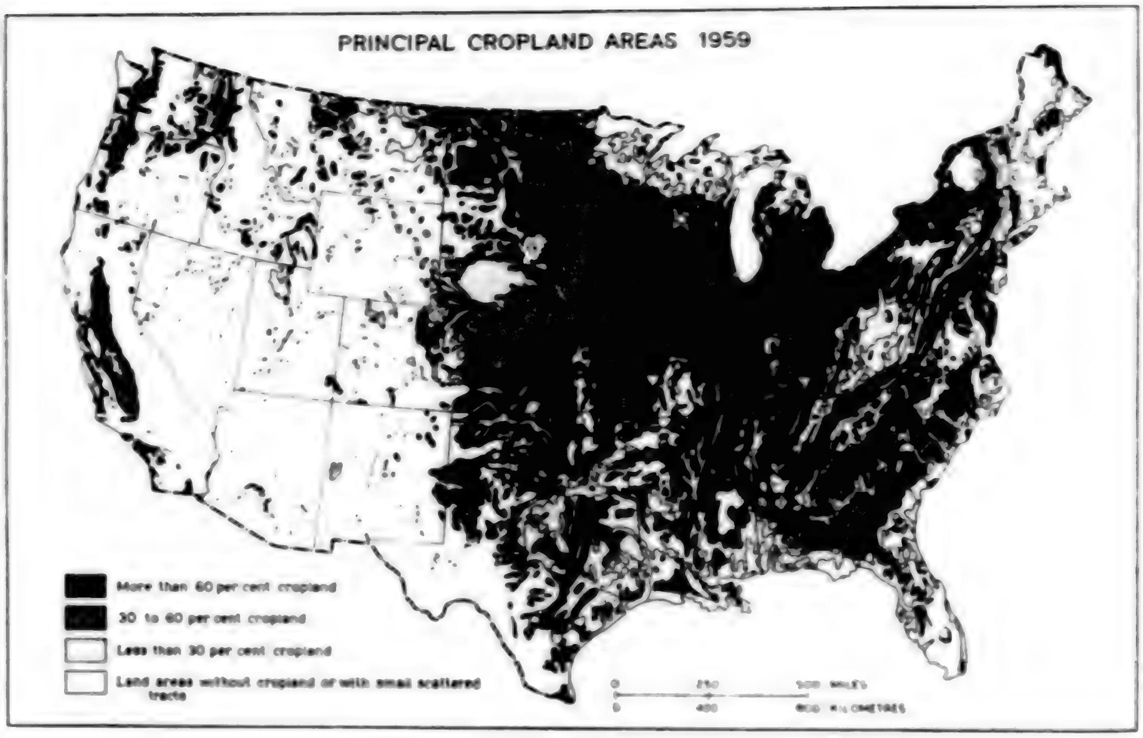

PRINCIPAL CROPLAND AREAS 1959
More than 60 per cent cropland
30 to 60 per cent cropland
Less than 30 per cent cropland
Land areas without cropland or with small scattered tracts
0 250 500 MILES
0 400 800 KILOMETRES

Fig. 5. Percentage of land in cultivation for the United States. this map helped to explain the 'anomalous' areas observed in the integrated NDVI map (Fig. 2). From Committee for World Atlas of Agriculture (1968). Authorized reproduction by Instituto Geografico de Agostini, Novara, Italy.

BEST COPY AVAILABLE

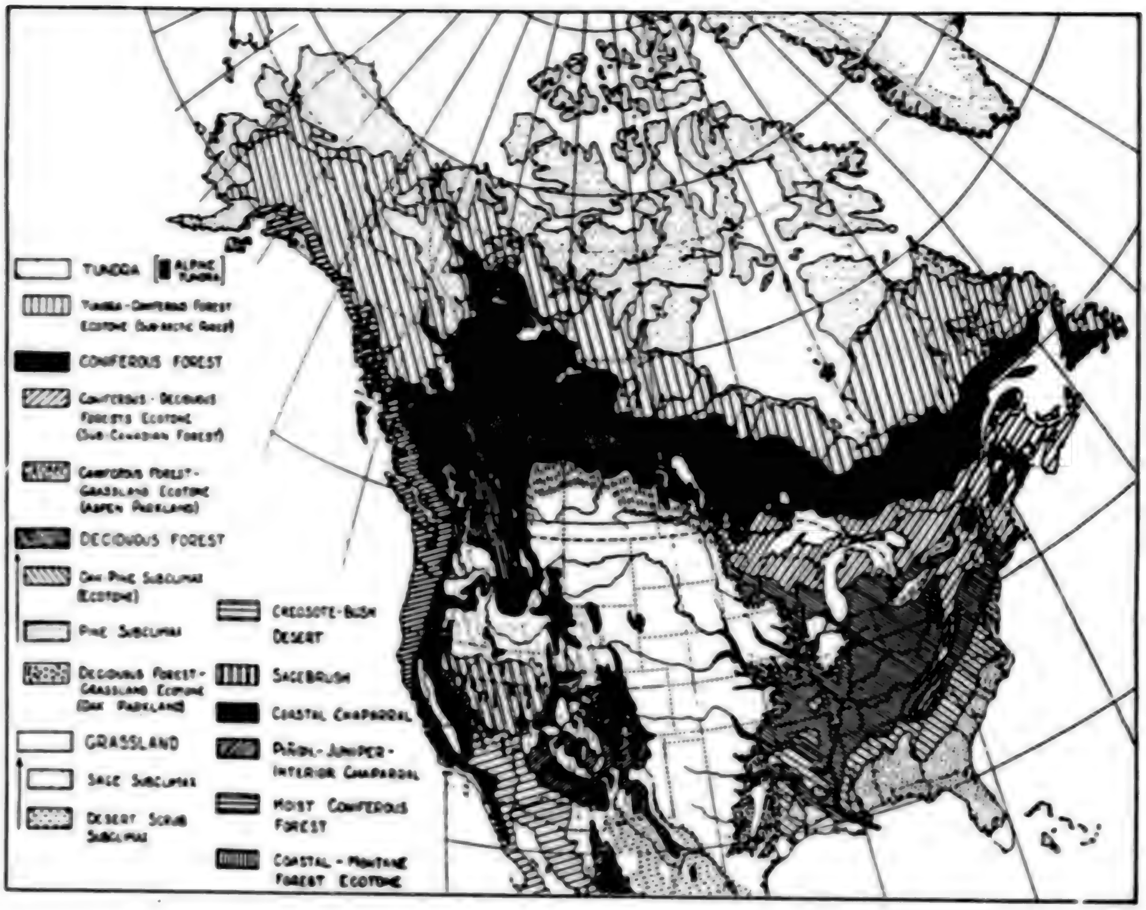

TUNDRA
ALPINE TUNDRA
TUNDRA-CONIFEROUS FOREST ECOTONE (SUBARCTIC FOREST)
CONIFEROUS FOREST
CONIFEROUS-DECIDUOUS FORESTS ECOTONE (SUB-CANADIAN FOREST)
CONIFEROUS FOREST-GRASSLAND ECOTONE (ASPEN PARKLAND)
DECIDUOUS FOREST
OAK-PINE SUBCLIMAX (ECOTONE)
PINE SUBCLIMAX
DECIDUOUS FOREST-GRASSLAND ECOTONE (OAK PARKLAND)
GRASSLAND
SAGE SUBCLIMAX
DESERT SCRUB SUBCLIMAX
CREOSOTE-BUSH DESERT
SAGEBRUSH
COASTAL CHAPARRAL
PIÑON-JUNIPER-INTERIOR CHAPARRAL
MOIST CONIFEROUS FOREST
COASTAL-MONTANE FOREST ECOTONE

Fig. 6. Distribution of major biomes in North America. This map was used to determine the natural vegetation types on the continent for the ∫NDVI-net primary productivity analysis. The detailed western vegetation subregions were grouped to form the woodland and scrub category (sage subclimax, sagebrush, coastal chaparral and pinon-juniper) and the desert category (desert scrub and creosote-bush desert). From Fundamentals of Ecology, 3rd ed. by Eugene P. Odum. Copyright (c) 1971 by Saunders College Publishing. Reprinted by permission of CBS College Publishing.

BEST COPY AVAILABLE

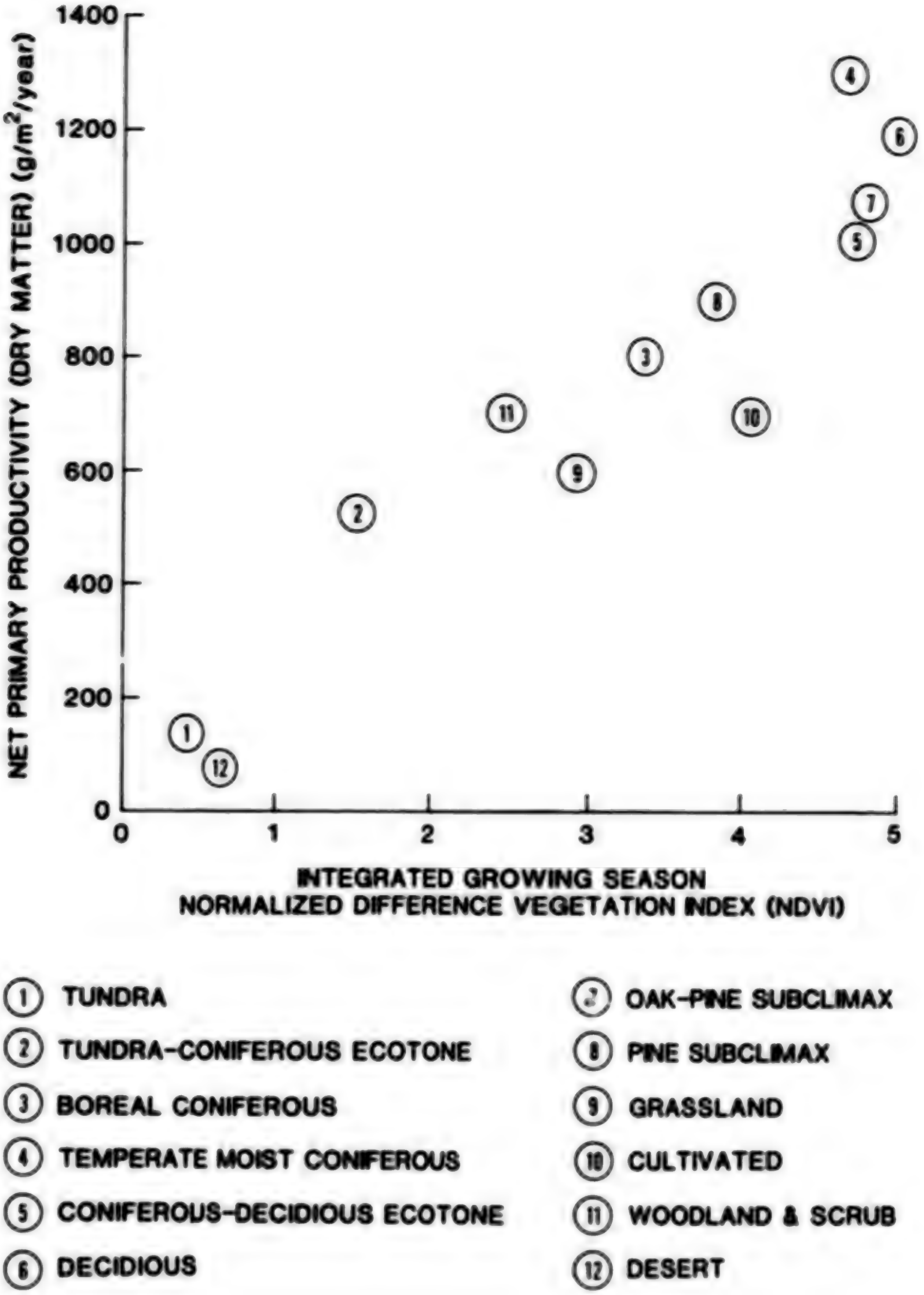


Fig. 7. Plot of biome-average $\int$NDVI measurements versus published mean biome net primary productivity rates. For each biome a well-distributed sample of $\int$NDVI measurements ($\sim$90 per biome) were used to compute the biome average. The net primary productivity figures are predominantly from Whittaker and Likens (1975), supplemented with values from Whittaker (1970), Rodin et al. (1975) and Lieth (1978). The explained variance (r^2) of the relation is 0.89. Exlcuding agriculture raises the r^2 value to 0.94.

BEST COPY AVAILABLE

CONCLUSIONS

The results from this analysis of NOAA-7 AVHRR observations of the North American continent show that these high temporal frequency, large area spectral measurements of the earth provide a major new source of information for investigations of terrestrial vegetation characteristics. Seasonal variations in the NDVI measurements agree with the known phenological patterns for natural and cultivated vegetation and, for natural vegetation, these temporal patterns vary in concert with climatic conditions which limit plant growth. Annually integrated patterns of NDVI measurements correspond to known continental patterns of net primary productivity. The effects of human cultivation are clearly noted, and these patterns agree with the known effects of agriculture on regional vegetation activity. Similar results have been derived for other continents (Tucker et al. 1985a, Justice et al. 1985). Use of AVHRR observations in macroscale studies of vegetation should significantly improve knowledge of global vegetation dynamics. Availability of several years of these high temporal frequency, globally consistent measurements will permit studies of interregional, interannual, and seasonal vegetation phenomena.

AVHRR observations represent an advance using satellite observations for vegetation research. The ability to observe the global distribution and dynamics of vegetation activity opens numerous new avenues of research. Improved understanding of the earth's terrestrial biosphere should result and at a time when concern is growing about human impact on resources.

ACKNOWLEDGMENTS

The research was supported under NASA Cooperative Agreement NCC 5-26. The assistance of Tom Goff and Virginia Kalb in processing the AVHRR data is appreciated.

LITERATURE CITED

Atjay, G. L., P. Ketner, and P. Duigneand. 1979. Terrestrial primary production and phytomass. Pages 129-181 in B. Bolin, E. T. Degans, S. Kempe and P. Ketner (editors), The Global Carbon Cycle. Scope Report 13, John Wiley, New York.

Asrar, G., M. Fuchs, E. T. Kanemasu, and J. L. Hatfield. 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. Agronomy Journal 87:300-306.

Blair, B. O., and M. F. Baumgardner. 1977. Detection of green and brown wave in hardwood canopy covers using multi-date, multispectral data from LANDSAT-I. Agronomy Journal 69:808-811.

Box, E. O. 1981. Macroclimate and plant forms: An introduction to predictive modeling in phytogeography. Tasks in Vegetation Science, 1 (H. Lieth, series editor). Dr. W. Junk, The Hague.

Colwell, R. N. 1956. Determining the prevalence of certain cereal crop diseases by means of aerial photography. Hildgardia 26(5):233-286.

Committee for World Atlas of Agriculture. 1968. World Atlas of Agriculture. Instituto Geografico de Agostini, Novara, Italy.

Curran, P. J. 1983. Multispectral remote sensing for the estimation of green leaf area index. Philosophical Transactions Royal Society London A 309:257-270.

Daughtry, C. S. T., K. D. Gallo, and M. E. Bauer. 1982. Spectral estimates of solar radiation intercepted by corn canopies. AgRISTARS Tech. Report SR-PZ-04236. Purdue University, West Lafayette, Indiana.

Deering, D. W., J. W. Rouse, Jr., R. H. Haas, and J. S. Schell. 1975. Measuring forage production of grazing units from LANDSAT MSS data. Pages 1169-1178 in 10th International Symposium on Remote Sensing of Environment. ERIM, Ann Arbor, Michigan.

Dethier, B. E. 1974. Phenology satellite experiment. Final report, tract NAS5-21781. Cornell University, Ithaca, New York.

Fung, I., K. Prentice, E. Matthews, J. Leaner, and G. Russell. 1983. Three-dimensional tracer model study of atmospheric CO_2: Response to seasonal exchanges with the terrestrial biosphere. Journal Geophysical Research 88:1281-1294.

Gates, D. M., H. J. Keegan, J. C. Schleter, and V. R. Weidner. 1965. Spectral properties of plants. Applied Optics 4:11-20.

Gray, T. L., and D. G. McCrary. 1981. The environmental index, A tool potentially useful for arid land management. AgRISTARS Rep. No. EW-N1-04076. NASA Johnson Space Center, Houston, Texas.

Greegor, D. H., and J. Norwine. 1981. A gradient model of vegetation and climate utilizing NOAA satellite imagery, Phase I; Texas transect. AgRISTARS Report No. FC-J1-04176. NASA Johnson Space Center, Houston, Texas.

Hatfield, J. L. 1983. Remote sensing estimates of potential and actual crop yield. Remote Sensing of the Environment 13:301-311.

Holben, B. N., and R. S. Fraser. 1984. Red and near-infrared sensor response to off-nadir viewing. International Journal Remote Sensing 5:145-160.

Holben, B. N., C. J. Tucker, and C. J. Fan. 1980. Assessing soybean leaf area and leaf biomass with spectral data. Photogrammetry and Engineering Remote Sensing 6:651-656.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.

Jackson, R. D. 1983. Spectral indices in n-space. Remote Sensing of the Environment 13:409-421.

Junge, C. E., and G. Czeplak. 1968. Same aspects of seasonal variation of carbon dioxide and ozone. Tellus 20:422-434.

Justice, C. O. 1983. Contribution of remote sensing to the inventory and monitoring of natural resources. Pages 362-366 *in* Proceedings, Renewable Resource Inventories for Monitoring Changes and Trends, Corvallis, Oregon. August 15-19.

Justice, C. O., J. R. G. Townshend, B. N. Holben, and C. J. Tucker. 1985. Analysis of the phenology of global vegetation using meteorological satellite data. International Journal of Remote Sensing 6:1271-1318.

Kauth, R. J., and G. S. Thomas. 1976. The tasseled cap - A graphic description of the spectral-temporal development of agricultural crops as seen by LANDSAT. Proceedings Symp. Machine Processing of Remotely Sensed Data, West Lafayette, Indiana.

Kidwell, K. A. 1979. NOAA polar orbiter users guide. Dept. of Commerce, Washington, D.C.

Knipling, E. B. 1970. Physical and physiological basis for the reflectance of visible and near-infrared radiation by vegetation. Remote Sensing of the Environment 1:115-119.

Krinov, E. L. 1947. Spectral reflectance of natural formations. Adak. Nauk, USSR, Laboratorica Aerometodov, Moxcow (Trans. by NEC of Canada, T1439, G. Belkov).

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society Special Publication No. 36, New York.

Kumar, M., and J. L. Monteith. 1981. Remote sensing of crop growth. Pages 134-144 *in* H. Smith (editor), Plants and the Daylight Spectrum. Academic Press, London.

Lieth, H. (editor). 1974. Phenology and seasonality modeling. Ecological Studies 8, Springer-Verlag, New York.

Lieth, H. (editor). 1978. Pattern of primary productivity in the biosphere. Benchmark Papers in Ecology, Vol. 8, Dowden, Hutchinson and Ross, Stroudsberg, Pennsylvania.

Mather, J. R., and G. A. Yoshioka. 1968. The role of climate in distribution of vegetation. Association American Geography Annals 58(1):29-41.

Monteith, J. L. 1977. Climate and the efficiency of crop production in Britain. Philosophical Transactions Royal Society of London B 291:277-294.

NASA/JSC. 1979. The LACIE symposium, Proceedings of technical sessions, Vols. I and II. NASA Johnson Space Center, Houston, Texas. 1125 pp.

National Oceanic and Atmospheric Administration. 1982. Monthly climatic data for the world. Sponsored by World Meteorological Organization, Vol. 35. National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, North Carolina. 172 pp.

Norwine, J., and D. H. Greegor. 1983. Vegetation classification based on AVHRR satellite imagery. Remote Sensing of the Environment 13:69-87.

Odum, E. P. 1971. Fundamentals of Ecology. 3rd Ed., W. B. Saunders, Philadelphia.

Olson, J., and J. A. Watts. 1982. Major world ecosystem complexes (map scale 1:30 M), included in W. C. Clark (editor), Carbon Dioxide Review 1982. Oxford University Press.

Ormsby, J. P. 1982. Classification of simulated and actual NOAA-6 AVHRR data for hydrologic land-surface feature definition. Geoscience and remote sensing GE-20:262-267.

Pearson, R. L., and L. D. Miller. 1972. Remote mapping of standing crop biomass for estimation of the productivity of the shortgrass prairie. Pages 1357-1381 in Proceedings of the Eighth International Symposium on Remote Sensing of Environment. Univ. Michigan, Ann Arbor.

Perry, C. R., and L. F. Lautenschlager. 1984. Functional equivalence of spectral vegetation indices. Remote Sensing Environment 14:169-182.

Richardson, A. J., and C. L. Wiegand. 1977. Distinguishing vegetation from soil background information. Photogrammetry Engineering and Remote Sensing 43:1541-1552.

Rodin, L. E., N. I. Bazilevich, and N. N. Razov. 1975. Productivity of the world's main ecosystems. in D. E. Reichle, J. F. Franklin, and D. W. Goodall (editors), Productivity of the World's Main Ecosystems. National Academy of Sciences, Washington, D. C.

Rouse, J. W. R. H. Haas, D. W. Deering, and J. A. Schell. 1974. Monitoring the vernal advancement and retrogradation (green wave effect) of natural vegetation. Final Rep. RSC 1978-4, Remote Sensing Center, Texas A&M University, College Station.

Schneider, S., and D. McGinnis, Jr. 1977. Spectral differences between VHRR and VISSR data and their impact of environmental studies. in Proceedings American Society of Photogrammetry, 43 Meeting 27 February to 5 March 1977, Washington, D. C.

Sellers, P. J. 1985. Canopy reflectance, photosynthesis, and transpiration. International Journal of Remote Sensing 6:1335-1371.

Shelford, V. E. 1963. The ecology of North America. University of Illinois Press, Chicago. 722 pp.

Steven, M. D., P. V. Biscoe, and K. W. Jaggard. 1983. Estimation of sugar beet productivity from reflection in red and near-infrared spectral bands. International Journal of Remote Sensing 4:325-334.

Thompson, D. R., and O. A. Wehmanen. 1979. Using LANDSAT digital data to detect moisture stress. Photogrammetry Engineering and Remote Sensing 45:201-207.

Townshend, J. R. G., and C. J. Tucker. 1981. Utility of AVHRR of NOAA-6 and -7 for vegetation mapping. Pages 97-107 in Matching remote Sensing Technologies and Applications Proceedings. Remote Sensing Society, London.

Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of the Environment 8:127-150.

Tucker, C. J., B. N. Holben, J. H. Elgin, Jr., and J. E. McMurtrey. 1981. Remote sensing of total dry-matter accumulation in winter wheat. Remote Sensing of the Environment 11:171-189.

Tucker, C. J., J. R. G. Townshend, and T. E. Goff. 1985a. Continental land cover classification using satellite data. Science 227:369-374.

Tucker, C. J., C. Vanpraet, E. Boerwinkle, and A. Gaston. 1985b. Satellite remote sensing of total dry matter accumulation in the Senegalese Sahel. Remote Sensing of the Environment 13:461-474.

Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380-1386.

Whittaker, R. H. 1970. Communities and Ecosystems. Macmillan, London. 162 pp.

Whittaker, R. H., and G. E. Likens. 1975. Primary production: The biosphere and man. in H. Lieth and R. H. Whittaker (editors), Primary Productivity of the Biosphere. Ecological Studies, 14, Springer Verlag, New York.

CHAPTER 10. LINKAGES IN HIERARCHICAL MODELS

D. L. URBAN AND R. V. O'NEILL
Environmental Sciences Division, Oak Ridge National Laboratory
Oak Ridge, Tennessee 37831

AND

H. H. SHUGART
University of Virginia, Charlottesville, Virginia 22903

Abstract. On-site measurements and remote-sensing imagery represent two scales from which landscape ecology can be approached. Hierarchy theory reconciles these two approaches in a paradigm embracing multilevel organization and provides guidelines for linking the approaches both empirically and in models. The theory suggests operational rules for (1) defining functional components of a phenomenon on a given space-time scale, (2) relating patterns and processes occurring on disparate scales, and (3) linking different but related phenomena via common variables at coincident scales. We discuss the prospects for modeling terrestrial landscapes as hierarchical systems.

INTRODUCTION

A goal of this workshop is to reconcile two approaches to the study of landscapes. The first approach, which proceeds 'from the bottom up,' attempts to assemble large-scale phenomena from smaller-scale components. Forest modelers generate forest dynamics by simulating the processes that affect the growth of individual trees and exemplify the 'bottom-up' approach (Shugart and West 1980). In contrast, a 'top-down' approach would analyze the pattern in a landscape and infer the processes that generated the pattern (Krummel et al., submitted ms). Remote-sensing studies have a clear application whenever one can link observed large-scale patterns to the smaller-scale processes. Our purpose in this paper is to explore a possible means of making this link.

The two approaches to studying landscapes represent two scales from which landscapes can be referenced. Landscapes can, in fact, be viewed from many scales. Landscape phenomena encompass patterns ranging in spatial scale from meters to thousands of kilometers, with dynamics observable over time scales of seconds to eons. Disturbances, regenerative processes, and environmental constraints at various scales interact to generate vegetation patterns at corresponding scales (Delcourt et al. 1983). Much of the apparent complexity of landscapes arises from this multiscaled pattern. Moreover, events at one scale are relatively disconnected from events at disparate scales. A description of the vegetation pattern at one scale of reference may not be appropriate to other scales. The successional patterns idealized in Clements' (1916) notion of a climatic monoclimax may apply, on the average, over large areas, but they do not predict the vegetation on any individual site (Gleason 1939). At the same time, the fine-scale details of a given site's vegetation are averaged out in the larger-scale description. This multiscaled, loosely coupled complexity demands a new conceptual model. A useful paradigm for landscape studies comes from hierarchy theory (Allen and Starr 1982; O'Neill et al., in press; Pattee 1973; Whyte et al. 1969).

In this paper we illustrate a hierarchical approach to the study of landscapes. While the paradigm is very rich as a conceptual model (Urban et al., in press), we believe that hierarchy theory may prove especially useful as a guide for structuring mathematical models to simulate multiscaled phenomena. Our intent here is to provide a brief overview of hierarchy theory as it applies to terrestrial landscapes and then to outline an approach to modeling landscapes so as to generate large-scale patterns from lower-level processes. We suggest that a hierarchical model may be the vehicle by which the 'bottom-up' and 'top-down' approaches to landscapes can be reconciled.

ELEMENTS OF HIERARCHY

A hierarchy is a partially ordered set in which the elements are ranked by asymmetric relationships among themselves. Various criteria might be used to order a hierarchy: higher levels may (1) be larger than, (2) behave more slowly than, (3) contain, or (4) control lower hierarchical levels (T.F.H. Allen, pers. comm.). In the case of terrestrial landscapes, all four criteria generally apply. The fact that landscapes are spatially nested (higher levels contain all the lower levels) provides for an especially rich conceptual and analytic framework (Allen and Hoekstra 1984).

Figure 1 illustrates an idealized hierarchical system. The first level comprises a number of small interacting components. Subsets of these components that interact much more among themselves than they do with components further removed can be aggregated to form the components of the next higher level. These, in turn, can be aggregated into a higher-level component, again based on their degree of interaction. The general rule is that within-aggregate interactions are much more frequent (or intense) than among-aggregate interactions. Importantly, the among-aggregate interactions at one level become the within-aggregate interactions of the next higher level. Thus, the dynamics of the system propagate mechanistically upscale, and the system is rate structured. In this example, the higher levels are also larger because they are composed of the lower-level components.

A forested landscape can be conceptualized as a hierarchical system (Fig. 2). The forest gap, the scene of gap-phase regeneration, is an easy choice for a reference level. Gaps have a spatial scale defined by the influence of a canopy-dominant tree and a natural frequency reflecting the life span of the dominant species (Shugart and West 1979; Shugart et al. 1981; Shugart 1984). Higher levels of a forest hierarchy can be aggregated from gaps, based on their degree of interaction. Important interactions include seed dispersal, nutrient flux, and so on. Note that because landscapes are spatially nested, it may often be convenient to use correlates or interactions, measured as similarity of attributes such as species composition, soil type, and so on, according to the

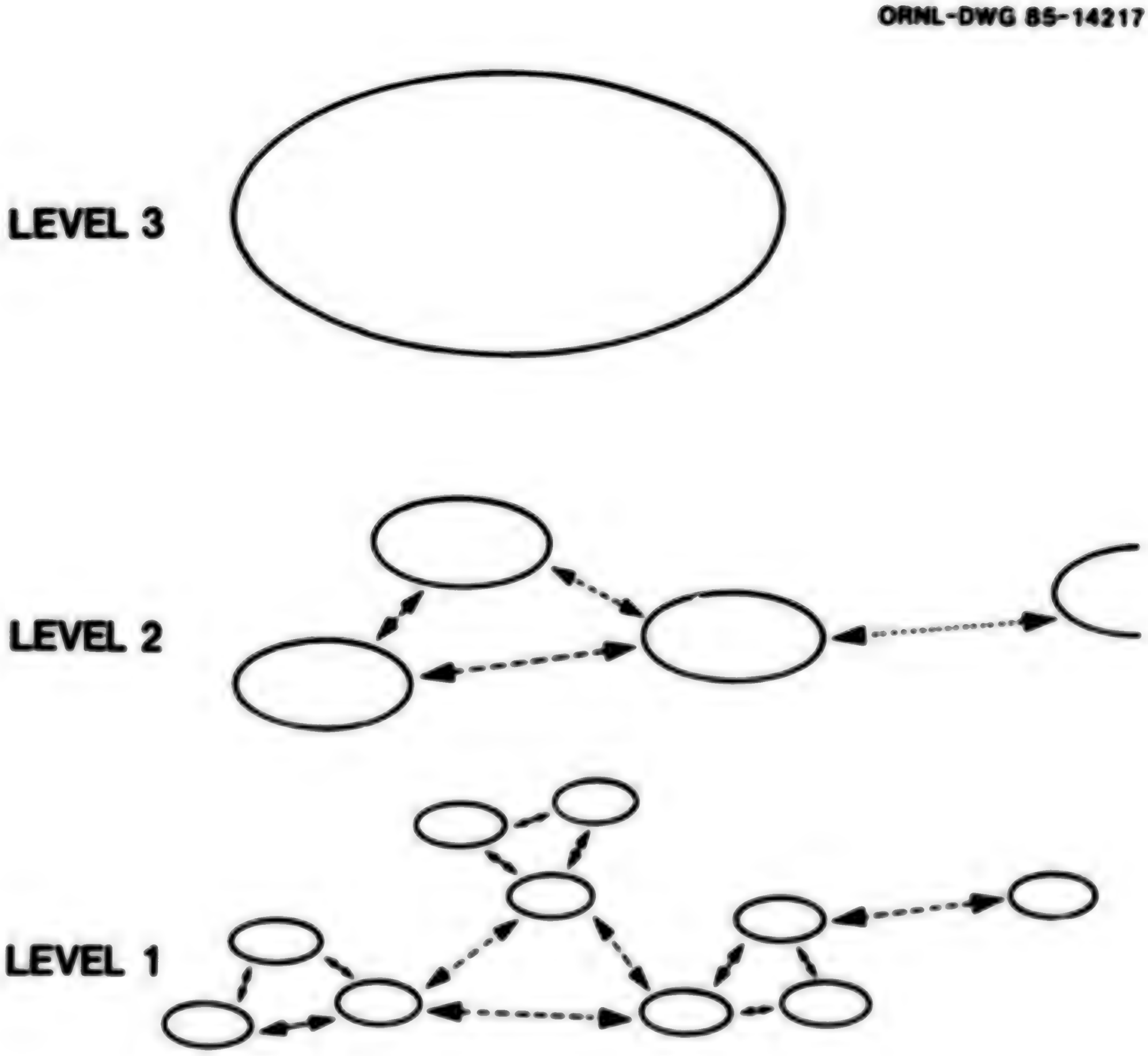


Fig. 1. Schematic of a generalized hierarchical system.

BEST COPY AVAILABLE

ORNL WS-40307

FOUR LEVELS OF A FOREST HIERARCHY

LEVEL	BOUNDARY DEFINITION	SCALE
LANDSCAPE	PHYSIOGRAPHIC PROVINCES; CHANGES IN LAND USE OR DISTURBANCE REGIME	10000s ha
WATERSHED	LOCAL DRAINAGE BASINS; TOPOGRAPHIC DIVIDES	100s–1000s ha
STAND	TOPOGRAPHIC POSITIONS; DISTURBANCES PATCHES	1s–10s ha
GAP	LARGE TREE'S INFLUENCE	0.01–0.1 ha

Fig. 2. Representation of a forested landscape as a hierarchy.

interactions of interest. Thus, stands can be aggregated from similar, interacting gaps; stands interact within watersheds; and landscapes are composed of interacting watersheds.

Note that the behavior observed at any level must be explained in terms of lower-level interactions (which propagate upscale) and higher-level context (which constrains downscale). Thus, gap dynamics are explained in terms of interactions among trees within the context of the gap's position in a stand, watershed, and on upscale. We can explain gap dynamics if we know which trees are present and the conditions under which they grow. This multilevel explanation is fundamental to hierarchical phenomena: given an event of interest, its mechanistic explanation lies in the interactions of the components of the next lower level; its significance, in the context of higher-level constraints (O'Neill et al., in press).

The multileveled approach to hierarchical phenomena is streamlined by the simplicity with which patterns and dynamics translate across levels. In general, a reference level only experiences patterns and dynamics that are similarly scaled. Lower-level dynamics are too fast to be seen as variables; they are experienced as integrated values or averages. Lower-level spatial patterns are seen as a blend. Reciprocally, higher-level dynamics are so slow that they are experienced as constants, and larger-scale spatial patterns are seen only as a uniform, local condition. Thus, the multileveled patterns and dynamics translate as averages, variables, and constants, according to the reference level. This translation across levels, an aspect of loose coupling (Simon 1973), effectively allows one to decouple a hierarchical system to study individual levels or subsystems separately.

Two aspects of hierarchy provide useful guidelines for making models to simulate multilevel systems, such as forested landscapes. The first is that realized behavior in a system is the consequence of the system's components' potential behavior being constrained by their context. Many successful models can be seen to include this structure (Allen and Starr 1982; O'Neill et al., in press). Indeed, any good model specifies the interacting components of the modeled system and the constraints under which those components interact. Hierarchy is of further use because the theory dictates the way components of multilevel systems should be linked. This is especially pertinent to our current objective, which is to construct models that can successfully link levels and work at disparate scales.

LINKAGES IN HIERARCHICAL MODELS

There are three kinds of linkages or couplings of interest in modeling a multilevel system, such as a terrestrial landscape. Horizontal links couple components at the same level by specifying the nature and degree of interactions among the components. Vertical links are those that connect adjacent levels in a hierarchy. A third kind of linkage is between two different hierarchies; that is, coupling two phenomena that are related to each other but whose representative hierarchies are not coincident.

Horizontal Links

The simplest model represents a set of functional components that interact on the same spatial and time scale but does not include components that act on other scales. This a perfectly legitimate modeling approach when the model is scaled so that the components of interest can be functionally isolated. This is what we refer to as decomposing a loosely coupled system (Simon 1973): isolating a level as an interesting subsystem. Constructing such a model requires that we (1) define the components of the model (which involves choosing the appropriate focal scale), (2) identify the interactions among the components, and (3) specify the extent to which the components interact. The phenomenon of interest dictates the nature of the components and the important interaction (Allen et al. 1984).

Components are delineated by steep gradients in interaction strength. In spatially nested systems, such as landscapes, interaction strength is often a function of distance; adjacent components interact more than components that are further removed. Importantly, the boundaries of the components at that level emerge from the observation set (the measurements on the dynamic of interest) and need not correspond to units that might be convenient to the modeler. Vegetation patches are defined by sharp gradients in species similarity (reflecting the dynamics of species replacement) and need not correspond to convenient units for packaging data.

Vertical Linkages

In a rate-structured hierarchy the couplings between adjacent levels are implicit in the horizontal (within-level) interactions. Subsets of strongly interacting components at one level are aggregated to become the components of the next higher level. Interactions among these aggregates derive from the comparatively weak interactions among the subsets of components that interact strongly at the lower level (see Fig. 1). Thus, the among-component interactions at one level become the within-component interactions at the next higher level, thereby linking the two levels. In particular, the dynamics of the higher level are generated mechanistically from below.

In a system that is not explicitly rate-structured, two levels can be coupled only if they have in common a phenomenon, such that the measured variables at each level differ only in grain (fineness of resolution) or extent (Allen et al. 1984). The levels can then be linked by simple transformations of the measures such as summation, averaging, or integration. One gains access to a higher level by extending an observation set in space or in duration to witness larger-scale patterns; a lower level is reached by increasing the resolution of measurements in order to resolve finer-scale patterns. Successional patterns emerge only if one tracks forest growth long enough to witness species replacement. Forest microhabitat pattern can only be resolved if one's measurements are sufficiently fine grained to record different microhabitats.

Linking Related Hierarchies

Two different hierarchies that are related can be linked if the same phenomenon occurs as a dynamic in each of the hierarchies; that is, if it occurs as a state variable in the models that represent each hierarchy. The hierarchies then can be linked at the level where the phenomenon co-occurs, the coincident level. Note that because the adjacent levels in either of the linked hierarchies can be reached by simple data transformations, the linkage actually involves six levels (three on each side), but only two of these need be coincident. Forest dynamics are related to climate but models of forests and climate can only be linked where they share state variables in common.

DISCUSSION

Our intent here has been to present an overview of a means by which two approaches to landscape ecology might be profitably reconciled. One approach, which we called 'bottom up' is comparatively fine grained (high resolution) but not extensive; the other ('top down') is rather coarse grained but very extensive. Our task is to develop a protocol for linking the two somewhere in the middle. More specifically, the problem is to find a means of relating biotic processes that we understand (describing our 'ground truth' data base) to larger-scale patterns that we can measure rather easily but have only recently attempted to explain. We suggest that a hierarchical approach may provide this protocol.

The first step in reconciling ground truth and remote sensing approaches is to identify functional patches, using both methods independently. The observation sets are very different for the two approaches (measures of trees or soil variables vs reflected radiance), but patches are defined by the same rigid criteria: steep gradients or break points in the measurements. We would expect that the 'bottom-up' approach could find several levels of patchiness, with the upper limit fixed by the logistics of data collection in the field. Ecologists simply cannot collect data over areas much larger than watersheds. Reciprocally, remote sensing cannot provide the amount of detail that field measurements permit, but remote imagery does have access to patterns that are orders of magnitude larger than the data accessible when using the former approach. As a second step, the functional components must be related via common state variables. Defining coincident levels for these variables links the two approaches. For forests or grasslands, leaf area index (or a correlate) may prove a useful linking variable, because the index (or a surrogate) can be computed using either onsite measurements or remote imagery. Coincident levels for such a variable should be derived from the observation sets rather than dictated a priori, but there are some likely candidates for convenient coincident levels. For example, LANDSAT's thematic mapper has a pixel size that roughly corresponds to the scale of a forest gap, and NOAA's AVHRR maps have units that might coincide with watersheds. It seems likely that the low-level (ground-based) and high-level (remote-sensing) approaches can be successfully linked on one or more scales. This link gives either approach access to the full hierarchy assembled by the two approaches, because adjacent levels can be reached by data transformations. While this procedure requires verification and testing, we believe the hierarchical approach to be sufficiently promising to warrant further attention in collaborative studies using existing ground-truth data bases and newer, technologically oriented approaches to ecology, including remote-imagery technology.

LITERATURE CITED

Allen, T. F. H., and T. W. Hoekstra. 1984. Nested and non-nested hierarchies: A significant distinction. Pages 175-180 in A. W. Smith, editor. Proceedings of the Society for General Systems Research. I. System Methodologies and Isomorphies. Intersystems Publ., Coutts Library Service, Lewiston, New York

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: Perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois.

Allen, T. F. H., R. V. O'Neill, and T. W. Hoekstra. 1984. Interlevel relations in ecological research and management: Some working principles from hierarchy theory. USDA Forest Service Gen. Tech. Rep. RM-110, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Institute Publ. 242. Washington, D. C.

Delcourt, H. R., P. A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: The spectrum of vegetation change in space and time. Quaternary Science Review 1:153-175.

Gleason, H. A. 1939. The individualistic concept of the plant association. American Midland Naturalist 21:92-110.

Krummel, J. R., R. H. Gardner, G. Sugihara, and R. V. O'Neill. Landscape patterns in a disturbed environment (submitted to Oikos).

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. A hierarchical concept of the ecosystem. Princeton University Press, Princeton, New Jersey (in press).

Pattee, H. 1973. Hierarchy theory. Braziller, New York.

Shugart, H. H. 1984. A theory of forest dynamics. Springer-Verlag, New York

Shugart, H. H., and D. C. West. 1979. Size and pattern of simulated forest stands. Forest Science 25:120-122.

Shugart, H. H., and D.C. West. 1980. Forest succession models. BioScience 30:308-313.

Shugart, H. H., D.C. West, and W. R. Emanuel. 1981. Long-term dynamics of forest ecosystems. American Scientist 69:647-652.

Simon, H. A. 1973. The organization of complexity. Pages 3-27 in H. H. Pattee, editor. Hierarchy Theory. Braziller, New York.

Urban, D. L., R. V. O'Neill, and H. H. Shugart. 1986. Landscape ecology: A hierarchical perspective. BioScience 36:000-000.

Whyte, L. L., A. G. Wilson, and D. Wilson, editors. 1969. Hierarchical structures. Elsevier, New York.

CHAPTER 11. LANDSCAPE ECOLOGY: SPATIAL DATA AND ANALYTICAL APPROACHES

J. R. KRUMMEL
Energy and Environmental Systems Division
Argonne National Laboratory, Argonne, Illinois 60439

Abstract. Understanding the dynamics underlying spatial pattern is a central problem in the study of ecology. The landscape, which explicitly incorporates the spatial properties of the environment, represents an appropriate spatial unit to address large-scale spatial heterogeneity. The study of landscape structure and function involves the use of data, analysis methodologies, models, and computer resources that have only recently become available to the scientific community. The development of remote sensing, digital data processing, geographic information systems, spatially-distributed parameter models, and techniques for quantifying landscape pattern provide new opportunities to analyze natural systems over large geographic areas. In this paper, I briefly outline some of these developments in the context of the methods and tools needed to explicitly incorporate scale and spatial pattern in the analysis of natural systems. By increasing the spatial scale, yet maintaining the integrity of a patterned environment, opportunities also exist to study environmental problems at larger spatial scales.

INTRODUCTION

Biological processes (reproduction, growth, and death) operate in the context of spatial pattern. Grazing patterns by large herbivores, prey refugia, plant succession, and species and genetic diversity all have important spatial components (Huffaker 1958, Holling 1966, May 1975). Understanding the dynamics underlying spatial pattern is a central problem in the study of ecology (Curtis 1959, Pielou 1977, Levin 1976). Theoretical studies (Cohen 1970, Steele 1974, Clark et al. 1978, Levin and Paine 1974, Jones and Krummel 1985) have demonstrated the importance of spatial considerations in energy flow, nutrient cycling, and population dynamics.

The large geographic scale of anthropogenic perturbations necessitates that spatial heterogeneity be considered to provide an integrated view of environmental problems (Krummel et al. 1984). The landscape represents the appropriate spatial unit to address large-scale spatial heterogeneity (Wilson and Willis 1975, Krummel and Dyer 1984). The landscape scale is large enough to include the spatial pattern that develops from the interaction of physical and biological forces (Basta and Bower 1982). Populations interact with other populations and the abiotic environment to produce patterns at the landscape scale. Indeed, the landscape as a unit of study is coalescing among researchers and land use managers (Burgess and Sharpe 1981, Deardon 1978, Forman and Godron 1981, Naveh 1982).

The study of landscape structure and function involves the use of data, methodologies, models, and computer resources that have only recently become available to the scientific community (Risser et al. 1983). Central to these developments is the idea that landscape analyses must explicitly incorporate the spatial pattern found in the environment. Indeed, while ecosystem analysis attempts to create "black box" explanations of spatial heterogeneity, landscape ecology must accept spatial pattern as a driving force in determining system function. While the analysis of spatial patterns in ecology has been an ongoing area of research (see Pielou 1977 or Patil et al. 1971), the complexity of natural boundaries continues to hinder the incorporation of landscape pattern in ecology (Loehle 1983). However, the development of remote sensing, digital data processing, geographic information systems, distributed parameter models, and techniques for quantifying landscape pattern provide new opportunities to analyze natural systems over large geographic areas. In this paper, I briefly outline some of these developments in the context of the methods and tools needed to explicitly incorporate scale and spatial pattern in the analysis of natural systems.

DATA AVAILABILITY AND MANIPULATION

Data Bases

Because of the importance of spatial data in basic and applied environmental studies, digital remote sensing (e.g., LANDSAT or processed aerial photographs), digital terrain, and other digital map data (e.g., soil groups or average rainfall) increasingly will be incorporated in the analysis of environmental problems. This quantitative information is a fortiori spatial (Harris 1981) and at the appropriate scale to test hypotheses that need to include large geographic areas but yet maintain the smaller scale, disaggregated pattern of environmental attributes. Examples of the latter are elevation, vegetation cover, or drainage networks. Remote sensing offers the unique ability to hold time constant but let space vary in a data collection scheme. In addition, the ability to manipulate digital information in a computer is essential for quantitative studies of spatial phenomena.

The Geographic Information System

A basic tool for the study of spatial relationships and the manipulation of digital data is a Geographic Information System (GIS). A GIS provides the necessary bookkeeping and analysis framework to work with spatial models and data. Like the Statistical Analysis System (SAS), which provides the computer resources to manipulate and statistically analyze data (Helwig and Council 1979), a GIS allows a researcher to evaluate the spatial properties of environmental attributes. The functions of a GIS include: (1) input and digitizing, (2) transformation and manipulation, (3) data management and extraction, (4) integration and analysis, (5) output and display. Also like SAS, a GIS requires a special set of software and hardware to provide the proper computational and display framework for the research endeavor.

A GIS has a number of unique capabilities that make the system appropriate for spatial analysis. For example, data input (e.g., land cover data for a multiparameter river basin model) can be done with a digitizing unit that records the location and type of data from hardcopy (i.e., aerial photograph) or digital tape (i.e., LANDSAT). Within a GIS one can merge spatial data sets, smooth point data to isopleth contours, combine grid-based data and polygonal data, and provide map output of the results of the analysis (either statistical or numerical). Examples of the types of problems that should incorporate a GIS framework include: (1) combining two different polygonal data sets, land cover and terrain, to produce a third spatial data set, erodability, that is input to a multiparameter hydrological model; (2) combining LANDSAT images with soil and rainfall parameters to display (map) a measure of forest productivity; or (3) digitizing old (ca. 1930) soil conservation maps and merging these data with current U2 data to plot historical land cover changes. To accomplish the above tasks (and more) requires both vector (polygonal) and raster (grid) data, as well as hardware and software that allow flexible file transfer between these two types of data structures.

It is also useful to distinguish between the two "generic" types of data that might exist in a GIS. To be useful in statistical or numeric models, the GIS will contain both relatively static and dynamic data sets. A static data base is generally composed of spatial and statistical data (e.g., soil types, terrain, or major vegetation associations) that change slowly over time; thus, this data base type requires little updating. For example, static data bases can provide (1) information on how the pattern in the environment (i.e., the mix of soil and vegetation types) can influence the movement of a disturbance or (2) data for evaluating the interaction (e.g., dose-response) between a disturbance and the potential receptors. Dynamic data bases consist of information that has a high degree of both temporal and spatial variation. Examples include up-to-date air- and water-quality conditions, animal population distributions, vegetation stress, or surface-water flow rates. While these data can be georeferenced to a specific point on the surface of the earth, the data require regular updating to maintain the integrity of the data base. In general, dynamic data bases provide important information on normal ambient fluctuations or unique disturbances to the natural system.

ANALYSIS OF SPATIAL HETEROGENEITY IN A REGIONAL FRAMEWORK

One of the key reasons for utilizing a GIS with digital data from remote sensing or other sources is to quantify and analyze the patterns that appear and relate these patterns to ecological processes that are primarily studied at smaller spatial scales. Central to this purpose is the need to develop parameters that define environmental pattern in a way that can be used to link pattern to biophysical processes. Only by connecting patterns to underlying processes can researchers begin to interpolate site-specific research to a larger regional setting (Burrough 1981). However, quantifying landscape pattern is only a part of the effort to link pattern with process. Process-oriented models must also explicitly incorporate spatial heterogeneity so that pattern is not a 'black box' component of system analysis. These are not new concepts in ecology (Watt 1947, Curtis

1956), but quantitative developments in ecological research explicitly analyzing landscape or regional patterns are relatively new to a majority of ecologists (Risser et al. 1983).

Potential Role of Fractal Analysis

Natural boundaries and patterns are so complex that most techniques developed to date detect only certain kinds of patterns (Loehle 1983). However, Mandelbrot's (1977) development of fractals has made it possible to quantify complex boundaries or patch shapes and relate these patterns to the underlying processes that may affect pattern complexity. Mandelbrot introduced fractal analysis (and the fractal dimension) as a method to study spatial phenomena that are partially correlated over many scales and are continuous but not differentiable. By applying the techniques of fractal analysis to environmental data, the possibility exists for quantifying the scales over which one can extrapolate site-specific data to larger geographic areas (Burrough 1981).

The appeal of fractal analysis in analyzing ecological patterns is the relative ease in which theory connects directly to empirical measurements (Mandelbrot 1977). To date, researchers have applied several techniques from fractal analysis to analyze natural shapes and boundaries (Mandelbrot 1977, Burrough 1981, Lovejoy 1982). By determining the fractal dimension for natural shapes (e.g., patches of deciduous forest or elevation boundaries) that occur over many size scales, one can begin to develop hypotheses about the spatial scale of the underlying processes that may control the size and shape complexity of landscape attributes. The spatial scale of these processes has important implications for the structuring of ecological systems (Bradbury et al. 1984). For example, Krummel et al. (submitted) calculated the fractal dimension of deciduous forest patches in the USGS Natchez, Mississippi, Quadrangle based on perimeter-area data from digitized aerial photographs. They found a significantly lower fractal dimension for small patches compared to the larger patches (Fig. 1) and that this difference was most likely related to scale distinctions between human disturbance and the natural biophysical processes that control forest succession. Below 60 ha the forest patches have regular shapes characteristic of patterns generated by survey and township divisions; above that patch size the patterns are more irregular and most likely set by physical processes (i.e., hydrology and terrain) that control plant succession.

Quantifying patterns in natural systems is complemented by the development of spatially explicit catchment runoff models (Beasley and Huggins 1981, Beven and Kirkby 1979, O'Loughlin 1981). These models forecast water runoff, nutrient flux, sedimentation, and erosion by including the pattern of land cover, soil, and topography in a drainage basin. Thus, the distributed parameter or contributing area nature of these models links ecosystem processes to the patterns found in the landscape. The driving force in these models is the movement of water as controlled by topographic properties. Soil and vegetation both mitigate and respond to the flux of water, nutrients, and sediment. For example, vegetation cover influences the evapotranspiration rate and, in turn, water runoff, while long-term equilibrium conditions in the hydrology of drainage basin constrain the succession of vegetation communities.

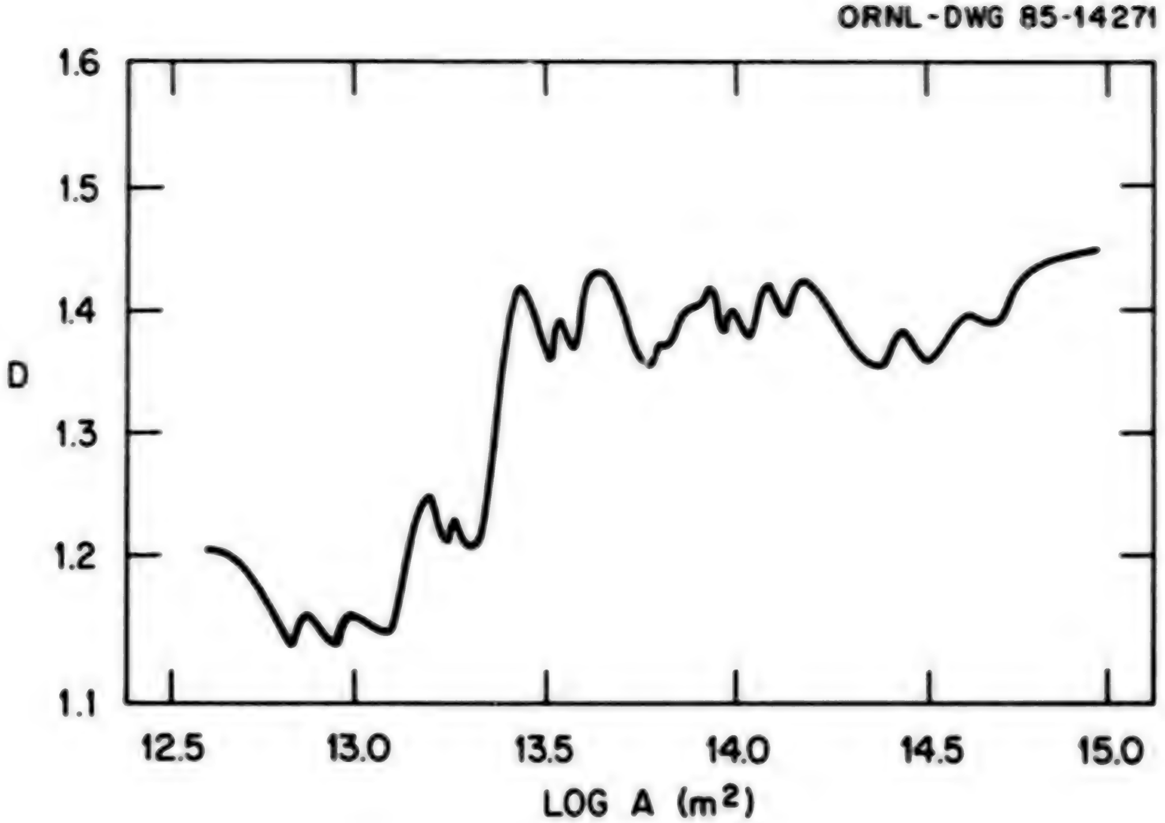


Fig. 1. Changes in the fractal dimension, D, as log area (m^2) increases as determined by successive regressions of log P on log A for the 505 deciduous forest patches in the Natchez, Mississippi, 1:250,000 Quadrangle (Krummel et al. submitted).

BEST COPY AVAILABLE

Since these types of models rely on the locational properties of parameters related to slope and land cover, a GIS is an important tool to provide computerized bookkeeping of the spatial attributes of the landscape. In addition, these models, in combination with digital terrain, soil and land cover data, allow researchers to begin extrapolating from well known, but site-specific, process studies (e.g., experimental watersheds) to larger geographic areas (Beasley and Huggins 1981). This extrapolation of site-specific information to broader geographic areas has important implications for the development of landscape ecology.

CONCLUSIONS

Research on disturbances and/or natural processes that operate over broad geographic areas must explicitly address problems of scale, uncertainty, and spatial heterogeneity. The concepts, models, and data types briefly mentioned here will support continued developments in landscape ecology. Researchers and managers can then begin to test hypotheses that directly connect environmental pattern to natural system processes. By increasing the spatial scale, yet maintaining the integrity of a patterned environment, opportunities also exist to study environmental problems at larger spatial scales. This is especially important, given the regional scale at which humans are altering the natural environment.

LITERATURE CITED

Basta, D. J., and B. T. Bower (editors). 1982. Analyzing natural systems resources for the future. Johns Hopkins University Press, Baltimore, Maryland.

Beasley, D. B., and L. F. Huggins. 1981. Answers - User's manual. Environmental Protection Agency Report 905/9-82-001, Chicago, Illinois.

Beven, K., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. Hydrological Science Bulletin 24:43-69.

Bradbury, R. H., R. E. Reichelt, and D. G. Green. 1984. Fractals in ecology: Methods and interpretation. Marine Ecology Progress Series 14:295-296.

Burgess, R. L., and D. M. Sharpe (editors). 1981. Forest island dynamics in man-dominated environments. Springer-Verlag, New York.

Burrough, P. A. 1981. Fractal dimensions of landscapes and other environmental data. Nature 294:240-242.

Clark, W. C., D. D. Jones, and C. S. Holling. 1978. Patches, movements, and population dynamics in ecological systems: A terrestrial perspective. Pages 385-432 in J. S. Steele (editor), Spatial Pattern in Plankton Communities. Plenum Press, New York.

Cohen, J. E. 1970. A Markov contingency table model for replicated Lotka-Volterra systems near equilibrium. American Naturalist 104:547-559.

Curtis, J. T. 1956. The modification of mid latitude grasslands and forests by man. Pages 721-736 in W. L. Thompson (editor), Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, Illinois.

Curtis, J. T. 1959. The vegetation of Wisconsin - An ordination of plant communities. University of Wisconsin Press, Madison, Wisconsin.

Deardon, P. 1978. The ecological component in land use planning: A conceptual framework. Biological Conservation 14:167-178.

Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. Bioscience 31:733-740.

Harris, R. 1981. Remote sensing. Pages 36-45 in Quantitative Geography: A British View. Rutledge and Kegan Paul, Boston.

Helwig, J. R., and K. A. Council. 1979. SAS User's guide. SAS Institute, Cary, North Carolina.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Memoirs of Entomological Society Canada 48:1-85.

Huffaker, C. B. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

Jones, D. W. and J. R. Krummel. 1985. The location theory of animal populations: The case of a spatially uniform food distribution. American Naturalist 126:392-404.

Krummel, J. R., C. C. Gilmore, and R. V O'Neill. 1984. Locating vegetation 'at-risk' to air pollution: An exploration of a regional approach. Journal Environmental Management 18:279-290.

Krummel, J. R., R. H. Gardner, G. Sugihara, R. V. O'Neill, and P. R. Coleman. Landscape patterns in a disturbed environment (submitted to Oikos).

Krummel, J. R., and M. I. Dyer. 1984. Consumers in agroecosystems: A landscape perspective. Pages 55-72 in R. L. Lowrance, B. J. Stinner, G. J. House (editors), Agricultural Ecosystems-Unifying Concepts. John Wiley and Sons, New York.

Levin, S. A. 1976. Spatial patterning and the structure of ecological communities. Lectures on Mathematics in the Life Sciences 81:1-35.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch information, and community structure. Proceedings of the National Academy of Sciences 71:2744-2747.

Loehle, C. 1983. The fractal dimension and ecology. Speculations in Science and Technology 6:131-142.

Lovejoy, S. 1982. Area-perimeter relation for rain and cloud areas. Science 216:185-187.

Mandelbrot, B. B. 1977. Form, change, and dimension. W. H. Freeman Press, San Francisco.

May, R. M. 1975. Patterns of species abundance and diversity. Pages 81-120 in M. L. Cody and J. M. Diamond (editors), Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts.

Naveh, Z. 1982. Landscape ecology as an emerging branch of human ecosystem science. Advances in Ecological Research 12:189-237.

O'Loughlin, E. M. 1981. Saturation regions in catchments and their relations to soil and topographic properties. Journal of Hydrology 53:229-246.

Patil, G. P., E. C. Pielou, and W. E. Waters (editors). 1971. Spatial patterns and statistical distributions. The Pennsylvania State University Press, University Park.

Pielou, E. C. 1977. Mathematical ecology. Wiley-Interscience, New York.

Risser, P. G., J. R. Karr, and R. T. T. Forman. 1983. Landscape ecology: Directions and approaches. Illinois Natural History Survey Special Publication No. 2, Champaign, Illinois.

Steele, J. S. 1974. Spatial heterogeneity and population stability. Nature 248:83.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:12-22.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages 522-534 in M. L. Cody and J. M. Diamond (editors), Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts.

CHAPTER 12. SUMMARY: "THE PRESENT AS THE KEY TO THE FUTURE"

M. I. DYER

AND

D. A. CROSSLEY, JR.
Department of Entomology, University of Georgia, Athens, Georgia, 30602

The preceding chapters cover topics within a broad subject area, ranging from ecosystem production parameters, to remote sensing technology, to the development of new ecological theories or paradigms, which will pave the way for new directions in coupling remote sensing and ecology. There is little or no doubt expressed about the need for such a major coupling program; it is just clear how such a program should be constructed because the interconnections between the diverse disciplines are tenuous.

The data bases and ongoing research projects at Coweeta Hydrologic Laboratory, H. J. Andrews and Hubbard Brook Experimental Forests, along with the strong background of Great Smoky Mountains National Park, clearly are among the best sites for structuring a coupled remote sensing and ecological program for temperate forests. The synopses for the three USDA Forest Service sites show that each has assembled state variable and process data on terrestrial and aquatic system interfaces for several decades. Each site has much the same type of information. Thus, a high degree of comparability of data exists. This synoptic data base allows for the testing of a variety of ideas, hypotheses, or equipment as plans for the coupling work unfold. The information about Coweeta presented by Swank and Crossley (Chapter 3) gives the reader a strong sense of the internal organization and design of the data bases. Franklin and Waring (Chapter 4), and Pierce and Siccama (Chapter 5), add viewpoints about their respective sites and also present the reader with a description of the type of background information available for H. J. Andrews and Hubbard Brook Experimental forests. Despite the fact that each research site is different in its physiognomy and specific vegetation, there are many similarities which present a strength for comparative studies. It is at once this commonality at one level of resolution and the major differences at other levels of resolution that provide a strong potential for an integrated program of study involving remote sensing. We know of no better place for learning how to describe, understand, and cope with spatial and temporal heterogeneity than with these three research sites. An additional strength appears when the Great Smoky Mountains Biosphere Reserve is factored into the overall equation. White and MacKenzie (Chapter 6) present a detailed analysis of the manner in which high resolution remote sensing approaches can be coupled to detailed knowledge of vegetation distribution and community processes on the ground. The Biosphere Reserve set formed by highly detailed watershed experiments at the nearby Coweeta Hydrologic Laboratory and both the larger and smaller scale approaches being taken in GRSM promises to give a picture of landscape function that is not yet available. Current model systems being used in forested landscapes and their possible extension (reviewed by Shugart and Smith, Chapter 7) give promise of new approaches which can be structured by development and adherence to hierarchy theory in ecological regimes. The idea of developing a modeling paradigm in system ecology which is analogous to the development of the compound microscope (later the "zoom" microscope) in biology is extremely interesting. The ability to examine an ecological problem at several levels with one model structure would be an important development. Urban et al. (Chapter 10) give a promising formula for developing the 'glue' for holding such complex studies together. It is clear from their comments that without the ability to relate complex interactions at several simultaneously operating levels of resolution, we may never have the potential for coupling remote sensing and ecological studies. Pastor and Huston (Chapter 8) provide an excellent example of how understanding basic processes in forested landscapes through the development of new modeling approaches can, in turn, aid our abilities to understand a larger system. Goward et al. (Chapter 9) show how one type of remote sensing program can be used to integrate similar concepts over large landscapes, while White and MacKenzie (Chapter 6) suggest ways to handle integration of ecological information when working on a high-resolution basis. Lastly, at an intermediate level, Krummel (Chapter 11) suggests how information developed at either high- or low-resolution bases might be transposed to areas other than those where the information was developed. The use of biogeophysical information data bases and fractal analysis, a relatively new mathematical paradigm, holds considerable promise and needs to be explored in much greater detail in the near future.

Ecological Problems in Temperate Forests

The workshop participants reflected on a large number of problems which must be factored into an integrated program to couple remote sensing and ecological studies. These problems ranged from questions about basic research in temperate forest ecosystems to environmental impacts and engineering involved with remote sensing. A large variety of ecological concerns and their attendant variables were identified, screened and placed into a matrix form (Table 1). Initial discussions developed about how these should be treated in terms of temporal and spatial scale (see Table 1 examples). Table 1 is not intended to be inclusive, but rather provides examples of the interactions of various environmental variables with ecological processes, temporal behavior, and problems of scale. Much of the discussion centered on the following:

1. The ability to define and adequately test problems with complex issues of temporal and spatial heterogeneity.

2. The ability to determine with reasonable accuracy current conditions within a landscape segment and then to extrapolate this information and its correlative procedure to neighboring areas.

3. The ability to determine how processes within a landscape segment relate to one another.

4. The ability to measure state variables and processes within a landscape segment using remote sensing methods.

Table 1. Matrix of relationships between major Ecological Problems in temperate forests and the variables used to study and express these concerns. Examples are given for a few cases which relate temporal and spatial scales needed to give detailed information about such ecological problems. The estimates serve for both basic ecological ground studies and remote sensing to determine how to couple the information.

	Variables													
Ecological Problems	Patch Size	Mass/unit area	Discolorization	C/N/S/P	Major elements	Heavy metals	OM-Dead	Soil water	Snow, frost	Canopy surface temperature	Topography	Geology	Soil charact.	Plant/water relationships
1. Vegetation patterns	2,3/V	2,3/V	3,6/V											
2. Vegetation/land-use change														
3. Tree growth decline	2,3,6/5													
4. Tree mortality														
5. Insect/disease impacts			3,6/3											
6. Climatological influences														
7. Event detection and scope														
8. Resource inventory/economics														
9. Animal habitat					2/3									
10. Fire hazard					?									
11. Atmospheric deposition														
12. Vegetation impact on hydrology							3,5,6,7/2,3							

Temporal Requirements

1. Once
2. Decade
3. Annually
4. Annual event
5. Seasonal
6. Episodic event (random)
7. Monthly
8. Weekly
9. Daily
10. Variable

Spatial Requirements

1. 4 km (AVHRR equivalence)
2. 1 km (AVHRR equivalence)
3. 80 m (older LANDSAT equivalence)
4. 30 m (Thematic Mapper equivalence)
5. 15 m specific requirements for
6. 1 m other remote sensing projects
7. Variable or for modeling needs

BEST COPY AVAILABLE

At this point, information is not adequate to choose among alternatives for any individual problem, let alone the entire ensemble. The ability to adjust or correct and fill in the matrix in Table 1 is a major task that must be taken on at a later date by both topic specialists and generalists with an interest in putting together a program where remote sensing and ecological studies can be coupled. In essence, this formulates the basis for what is now popularly being considered as a global change program for many aspects of the biosphere (NRC 1986). We stated above that information in Table 1 is extensive, but we make no claim that it is all inclusive. In this respect, we believe this is a major start for future attempts to elaborate the information outlined initially in the matrix. It is likely much information already exists for some of the cells; however, for many subjects, such as the fundamental ecosystem concept of defining mass per unit area, new projects will have to be designed to assemble the needed information for both ecological and remote sensing purposes. Other subjects are even less replete with available information, yet constitute crucial aspects of an overall program for coupling information. An example is soil water, a relatively well-known subject in some instances, but for remote sensing and critical ecosystem function, a subject with less than well- developed understanding. Many other equivalent examples are pertinent. In one respect this matrix approach promises to refocus opinions about the organization of current information and the development of priorities for obtaining new information in new programs.

Remote Sensing Technology

Even though representatives of agencies promoting the use of remote sensing (viz. NASA, USDA, USDI, and others) and several investigators who have used remote sensing extensively were present at the workshop, remote sensing technology was not a central focus. A great deal of information has been developed in remote sensing of the environment (see Colwell 1983), and several NASA publications present synopses of current hardware and new programs planned for the next decade (NASA 1984). Thus little attention is being given to this subject here.

The main feature which emerged from the workshop is that ecologists and those utilizing or designing remote sensing projects must pay more attention to temporal and spatial scales. The papers by Urban et al. and White and MacKenzie call particular attention to this fact. Botkin et al. (1984) give a field example of how difficult and expensive it is to cope with scale problems in a remote sensing study. (A summary of this work was presented at the workshop, but is not included in this volume.) It was obvious to all participants that, despite the fact there were several investigators working actively with AVHRR and Thematic Mapper data, even in some of the better developed projects being planned there are serious mismatches in scale. We underscored the importance of scale problems earlier and have noted those chapters contributing to this subject. We can only urge that a great deal more attention be given in the future to this subject, particularly in view of the focus we believe that Table 1 provides for the development of this subject area.

Uncertainty Analysis and Aggregation Problems

The expression of variance in laboratory and field studies is an inherent part of our modern biological and ecological world, thanks to decades-long development of mathematical and statistical methods. The subject is especially important in determining relationships in large systems. Originally the focus was on observations of individual organisms or processes, but now more and more our attention is turned toward observations on groups or aggregations. Thus, it has been necessary to invoke model representations of the world from which we extract the individual measurements. This development has required that we reorganize our thoughts on the subject of uncertainty where data--and models for expressing meaning of those data--are used (Gardner in press). Instead of having discrete units we now must consider assemblages, or rate processes that often are smoothed out or statistically skewed. Thus, it is not a simple task to show cause and effect relationships for many biological and ecological questions.

New work is needed for understanding relationships in complex ecosystem studies, such as those described at the four Biosphere Reserves cited in this volume. The new techniques for understanding uncertainty which Gardner (in press) has discussed must be carefully investigated in these large integrated watershed-level or ecosystem- level efforts. To date, these techniques have been applied to a variety of problems: radiological assessment (Hoffman and Gardner 1983, O'Neill et al. 1981); generic problems dealt with by ecological models (O'Neill and Gardner 1979); assessment models (Downing et al. 1985); stream ecosystem models (Gardner et al. 1981); marsh hydrology (Gardner et al. 1980a); global carbon cycling models (Gardner et al. 1980b); and predator-prey models (Gardner et al. 1980c). In all instances, information, which included data banks, was utilized along with a variety of models to provide an in-depth assessment of a particular problem. Even though much emphasis was on ways to assess uncertainty in modeling studies not specifically on data-oriented studies, the lesson for the future is clear. Studies involving models should not be divorced from data, particularly during validation and use of those models for planning or developing management alternatives in temperate forest ecosystems. Thus, we must address both data-oriented studies, such as long-term monitoring and field experiments and associated laboratory experiments, and modeling studies simultaneously. The lessons resulting from uncertainty analysis using modeling approaches suggest we have far to go in learning about uncertainty involving field and laboratory data. In the future, modeling and data collection must be integrated from the outset in ecosystem-level programs, particularly if we are to couple ground-level information with information taken from sensors on airplane or satellite platforms as called for in the NASA EOS program (NASA 1984).

A good example for developing and utilizing ecosystem-level uncertainty studies lies in extrapolating information from point sources to a spatially large scale. As Krummel (Chapter 11) pointed out, it is necessary to make this extrapolation if we are to develop a robust discipline in regional or global ecology, and a variety of approaches will be necessary. For economic reasons, if nothing else, it simply is not possible to repeat studies uniformly over large expanses of space, or over all time periods necessary to represent any given problem. Therefore, we need the ability to make reasonable extrapolations of point-source data, which we can agree are state-of-the-art, to other areas. The key question after we have made these extrapolations, are the new predictions representative of the area? The approaches put forward by uncertainty analysis and new validation programs will help answer this all-important question.

Also coupled with the uncertainty analyses is the question of how one should aggregate information to avoid problems with error (Gardner et al. 1982). Because complexity forces ecologists to deal with aggregates at some point, attention must be given to the way error affects the ability of an investigator to assemble meaningful descriptions of cause and effect in large systems. As we stated above, these approaches must be considered seriously for new large-scale programs where ecological and remote sensing data are being coupled.

The Needs for Archiving Information

One of the most important subjects identified in the workshop dealt with the archiving of past, present, and future data and information in programs coupling remote sensing and ecology. Archiving is particularly important for the programs at the Biosphere Reserve sites we focus on in this report, as well as for NSF-sponsored Long-term Ecological Research (LTER) performed at Coweeta Hydrologic Laboratory, H. J. Andrews, and nine other sites scattered around the United States (Michener 1986). Archiving information should be explicitly considered as new programs, such as a National Biological Survey (NBS) (Kim and Knutson 1986), are developed. The needs and opportunities for reciprocal benefits to both remote sensing technology and ecological research are immense. Techniques of archiving information must be developed so that both remote sensing and ecosystem analysis can derive mutual benefit. These LTER and Biosphere Reserve sites provide exceptional opportunities or interpretation ('ground truth') of imagery and have associated with them a cadre of scientists best suited for the scope of work needed. Contemporary ecological issues, as noted earlier, require the various scales of observations that remote imagery can provide. Thus, the development of long-term, continuous coverage is of exceptional importance.

Key issues that must be addressed are (1) future data acquisition, (2) archiving of past, current, and future imagery, and (3) education.

Future Data Acquisition. Important future remote imaging needs for the coupling programs include (1) continued NOAA AVHRR coverage at both 1- and 4-km scales, (2) continued LANDSAT Thematic Mapper (TM) coverage, (3) development of a pointable device in connection with the future EOS (Earth Observing System, NASA 1984), and (4) development of adequate geographic information systems (GIS). AVHRR provides frequent, low resolution coverage, giving unsurpassed coverage of large-scale, long-term events. LANDSAT imaging must be continued at those areas currently collecting it and commenced at those which as yet do not have it, and a high rate of acquisition should be maintained because its high resolution is necessary for many ecological issues. A portable device is needed for detecting and studying episodic and other unexpected events. The geographic information system is essential for comparison of remote and ground-based information and is a data base which should rise to preeminence in the next decade.

Archiving. Archiving of past, present, and future remote imagery is imperative. Immediate needs are (1) identification and archiving of the 1-km data from the NOAA 7 satellite from July 1981 to the present and (2) identification, copying, and archiving of the LANDSAT Thematic Mapper data from 1972 to the present. These data are extremely important because they represent the only decades-long time series for remote sensing of the land. A decade is a minimal time for detection of some important ecological changes and dynamic patterns. Pre-4-km NOAA 7 data are already being saved. Long-term, continuing archiving needs include the NOAA 7 data at both scales and the LANDSAT TM imagery. Ensuring that these data are conserved is a joint responsibility of NASA and the research groups at the major sites discussed in this report. Archiving is best done at locations where there is institutional capability of utilizing the data.

Education. A minimal number of institutions with capabilities of processing and utilizing remote imagery must be maintained to avoid any decline in the potential for developing a program for archiving. An appropriate number and geographic distribution of sites needs to be identified and subsequently supported. Support for these institutions should include repositories for the data as well as for centers of excellence dealing with all phases of the problem. Includea should be modeling, basic studies, education and outreach, and programmatic integration.

Relationships to Other Programs. Earlier we stated that the development of archiving for the temperate forest ecosystems that have had a long history would be important for other programs. The two sites that are associated with the National Science foundation Long-Term Ecological Research Program are already part of one of these networks (Michener 1986). Such information is also picked up by those utilizing the Geoecology Program (Olson et al. 1980) at Oak Ridge National Laboratory. Perhaps the most ambitious proposal is that of the National Biological Survey (Kim and Knutson 1986). The basic plan, once implemented, will be to include extant and new data sets from contributing field stations and research throughout the United States. Many subjects are being considered, ranging from taxonomic keys to ecosystem-level inputs, for many different purposes (Dyer and Farrell 1986). The list of agencies expressing interest in a centralized National Biological Survey covers most federal and state agencies. Thus, we feel that if the NBS is developed, a strong linkage to this effort ought to be explored early in the developmental stage. Not only could the approach and expertise being regarded for the NBS help the temperate forest sites designing new ecological and remote sensing studies, the information obtained from those studies would likewise be invaluable to the NBS concept.

New Developments

Much of the work done to date utilizing remote sensing is centered around pattern analysis of state variables on the ground, such as topographic features, green leaf distribution, location of bodies of water, or stressed vegetation. While this approach has been extremely useful and successful in the past decade and a half, it has become apparent that a shift away from this type of usage will be necessary if we are to develop remote sensing to its fullest potentials and couple its findings with those of ecology. For instance, Running (1986) and Running et al.

(1986) have suggested new ways to utilize green leaf biomass estimates emanating from Thematic Mapper and AVHRR programs. This approach, which develops a simple but basic model, can add significantly to interpretations of 'greenness' indices reported to date (cf. Tucker et al. 1985). Indeed, in this volume, both Olson (Chapter 2) and Goward et al. (Chapter 9) discuss essentially similar equations and approaches. Beyond that, ecologists need to turn to other robust modes of expressing ecological function, such as the influence of water in ecological exchanges, or the key major nutrients in ecological and landscape questions. By shifting away from the state variable/biomass emphasis toward the examination of processes by new remote sensing methods, we can introduce a major step forward in the science of coupling these two subject areas. Then, not only could patterns of biota be discerned, but their inherent rates of change per unit area per unit time could be determined. Once we arrive at that threshold, the development of the 'glue' through dynamical modeling discussed earlier could proceed. At the workshop, initial discussions of this potential suggested new approaches (Waring, personal communication), and since then reports about the potential of measuring N remotely with AIS (Airborne Imaging Spectrometer) have been published (Goetz et al. 1985, Waring 1985, Spanner et al. 1985, Waring et al. 1986). Should this approach be successful, then a new level of robustness in remote sensing/ecological studies would ensue. Models of C/N flux could give us a great advantage in determining dynamics of forested ecosystems (the same can probably be said about other ecosystems as well). The ability for analogous developments with water relations in various ecosystems, or other elements that have strong ecological ties would enhance the potential for the coupling studies even more. However, a great deal of basic research needs to be carried out, and new ideas need to be developed and tested. All of this work will require a great deal of background information and experience, much of which exists at the Biosphere Reserve sites discussed in this report.

RECOMMENDATIONS

Some of the recommendations emerging from the workshop, other than those about scientific programs noted earlier, centered about the types of individuals and agencies that should be considered for putting together the work coupling remote sensing and ecological studies. Certainly, as has been noted often, the four sites featured in this report have an important cadre of scientists and technicians who can handle many phases of the work. In addition, new principal investigators, post doctorates, and graduate students will be needed to provide basic ground-level ecological information testing some of the ideas and procedures promoted in this workshop report. These investigators will need to work closely with those in government laboratories and universities with expertise in remote sensing design and procedures. This suggests to us that a large interdisciplinary task force is needed to address the problems laid out here for doing work in temperate forests.

In order to carry out this work, some coordination and centralization of research support is needed, possibly by some branch of the Federal Government. Members and representatives of The National Science Foundation, Man and the Biosphere, the National Aeronautics and Space Administration, the U.S. Department of Agriculture, the National Oceanographic and Atmospheric

Administration, and the U.S. Department of Interior will bear main responsibility for this planning work. Once there is a plan, then investigators, mainly from university and government laboratories, can propose specific work to be reviewed by the peer community and representatives of the funding agencies. In this way, the best scientific input can be developed in the most efficient and cost-effective manner possible.

This work has strong international overtones when we consider future development programs. A large temperate forest exists outside the U.S. borders, even though the United States has some of the most active programs that give the best source of site-specific information needed for the coupling program. For example, the extensive dieback phenomenon in European forests lends itself to monitoring and analysis by remote sensing, while at the same time information from North America can be applied to the problem. Forested areas elsewhere can benefit greatly from an intensive program in the United States, but there will have to be plans laid for validating the results obtained from the intensive-site work. By enlisting aid from Europe and Asia, a stronger program can be made in the future. The Man and the Biosphere Program, located in the Department of State, can be quite instrumental in paving the way for developing this long-range goal on an international basis, and we recommend strongly that its potential be examined closely by MAB administrators and advisors.

LITERATURE CITED

Botkin, D. B., J. E. Estes, R. M. MacDonald, and M. V. Wilson. 1984. Studying the earth's vegetation from space. BioScience 34:508-514.

Colwell, R. N. (Editor). 1983. Manual of Remote Sensing. American Society of Photogrammetry. Sheridan Press, Falls Church, Virginia.

Downing, D. J., R. H. Gardner, and F. O. Hoffman. 1986. An examination of response-surface methodologies for uncertainty analysis in assessment models. Technometrics 27:151-163.

Dyer, M. I. and M. P. Farrell. 1986. Development of research information systems: Concepts and practice. Pages 119-132 in K. C. Kim and L. Knutson (editors) Foundations for a National Biological Survey. Allen Press, Inc., Lawrence, Kansas.

Gardner, R. H. (in press). Error analysis and sensitivity analysis in ecology. in M. Singh (editor) Encyclopedia of Systems and Control, Pergamon Press, London.

Gardner, R. H., D. H. Huff, R. V. O'Neill, J. B. Mankin, J. Carney, and J. Jones. 1980a. Application of error analysis to a marsh hydrology model. Water Resources Research 16:659-664.

Gardner, R. H., J. B. Mankin, and W. R. Emanuel. 1980b. A comparison of three carbon models. Ecological Modelling 8:313-332.

Gardner, R. H., R. V. O'Neill, J. B. Mankin, and D. Kumar. 1980c. Comparative error analysis of six predator-prey models. Ecology 61:323-332.

Gardner, R. H., R. V. O'Neill, J. B. Mankin, and J. H. Carney. 1981. A comparison of sensitivity analysis and error analysis based on a stream ecosystem model. Ecological Modelling 12:173-190.

Gardner, R. H., W. G. Cale, and R. V. O'Neill. 1982. Robust analysis of aggregation error. Ecology 63:1771-1779.

Goetz, A. F. H., G. Vane, J. E. Solomon, and B. N. Rock. 1985. Imaging spectrometry for earth remote sensing. Science 228:1147-1153.

Hoffman, F. O. and R. H. Gardner. 1983. Evaluation of uncertainties in environmental radiological assessment models. Pages 11.1-11.51 in J. E. Till and P. R. Meyer (editors) Radiological Assessment: A Textbook on Environmental Dose Assessment. U.S. Nuclear Regulatory Commission, Washington, D. C. NUREG/CR-3332, ORNL-5968.

Kim, K. C. and L. Knutson (Editors). 1986. Foundations for a National Biological Survey. Allen Press, Inc., Lawrence, Kansas.

Michener, W. K. (Editor). 1986. Research Data Management in the Ecological Sciences. University of South Carolina Press, Columbia, South Carolina.

NASA. 1984. Earth observing system. Volume I, Part I Working Group Report. TM-86129 NASA/Goddard Space Flight Center, Greenbelt, Maryland 20771.

National Research Council. 1986. Global Change in Geosphere-Biosphere: Initial Priorities for an IGBP. National Academy Press, Washington, D.C.

Olson, R. J., C. J. Emerson, and M. K. Nungesser. 1980. Geoecology: A county-level environmental data base for the conterminous United States. ORNL/TM-7351, Oak Ridge National Laboaratory, Oak Ridge, Tennessee.

O'Neill, R. V. and R. H. Gardner. 1979. Sources of uncertainty in ecological models. Pages 447-463 in B. P. Zeigler, M. S. Elzas, G. J. Kliv, and T. I. Oren (editors) Methodology in Systems Modelling and Simulation. North Holland Publishing Company.

O'Neill, R. V., R. H. Gardner, F. O. Hoffman, and G. Schwarz. 1981. Parameter uncertainty and estimated radiological dose to man from atmospheric ^{131}I releases: A Monte Carlo approach. Health Physics 40:760-764.

Running, S. W. 1986. Global primary production from terrestrial vegetation: Estimates integrating satellite remote sensing and computer simulation technology. Pages 000-000 in A. A. Orio and D. B. Botkin (editors) The Science of the Total Environment, from the conference, Man's Role in Changing the Global Environment, Venice, Italy, October 21-26, 1985. Elsevier Publishing Company, Oxford.

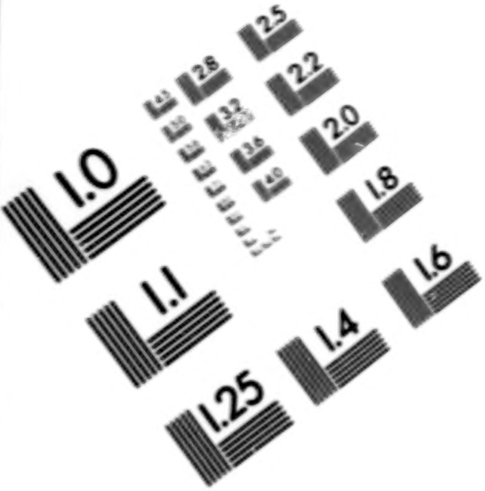
Running, S. W., D. L. Peterson, M. A. Spanner, and K. B. Teuber. 1986. Remote sensing of coniferous forest leaf area. Ecology 67:000-000.

Spanner, M. A., D. L. Peterson, W. Acevedo, and P. Matson. 1985. High resolution spectrometry of leaf and canopy chemistry for biogeochemical cycling. Pages 92-99 in G. Vane and A. F. H. Goetz (editors) Proceedings of the Airborne Imaging Spectrometer Data Analysis Workshop. Jet Propulsion Laboratory Publication 85-41.

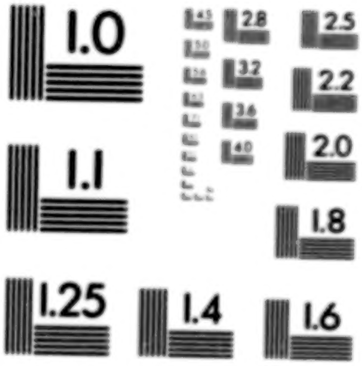
Tucker, C. J., J. R. G. Townshend, and T. E. Goff. 1985. African land-cover classification using satellite data. Science 227:369-375.

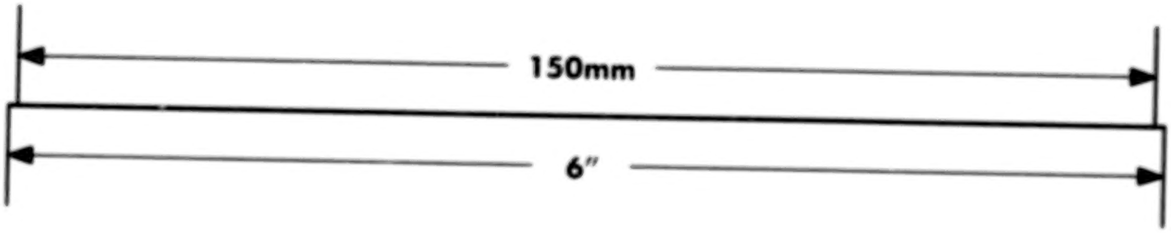
Waring, R. H. 1985. Precursors of change in terrestrial ecosystems. Pages 000-000 in Remote Sensing in Forestry and Range Management. Pecora 10 Symposium, Fort Collins, Colorado, August 20-22, 1985.

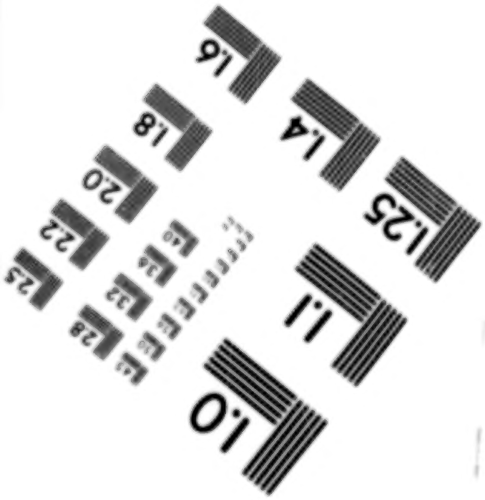
Waring, R. H., J. D. Aber, J. M. Melillo, and B. More III. 1986. Precursors of change in terrestrial ecosystems. BioScience 36:000-000.



UNITED STATES OF AMERICA
GOVERNMENT PRINTING OFFICE







END

FILMED

12-23-88